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Toys of Indian Children

Although portrayed as an unemotional people in much popular fiction, the American Indian was and is an enthusiastic, spirited, involved individual. As an adult, he thoroughly enjoyed all sorts of games, sports, and contests. Activities that displayed his prowess and skill were as favored as those on which he could wager. These attitudes toward play were nurtured from childhood when participation in games and playing with toys occupied much of a child's time. As Indian people came more frequently in contact with each other and with traders, missionaries, and settlers, their games and toys increasingly attracted attention. Some of these were modifications of ideas then recently acquired. Others stretched from antiquity.

Games were popular pastimes and youngsters indulged in a wide variety of these. Some games were restricted to adults, some were only for men, and some were only for women. Children never joined in these. Frequently games, even for children, were played only at certain seasons or specific times of the year, as at religious ceremonies or particular celebrations. Children, however, had toys—playthings which didn't necessarily require the participation of others—with which they could occupy themselves at any time. According to F. W. Hodge, there were three classes of such toys: those for attracting, soothing and amusing infants; those invented or appropriated by children for their own use; and those supplied by adults for educational, religious, or esthetic motives.¹

A child's earliest toys were those hung from the bow of his cradleboard. Strings of animal claws, teeth, or small white shells were frequently attached and within reach of the infant. Small animal skeletal heads might also be included or substituted. A baby's cradle toy could consist of several duck craniums, strung by the bills on a length of buckskin. In early times many mothers tied to the baby's wrist some small object which the child could put into its mouth but which was too large to swallow. An unusual toy described by a Menominee of the Eastern Woodlands "consisted of the leg of a freshly killed deer, a muscle left so that an older person could pull it, thus causing the toes to move for the amusement of the child."² Birds and animals, such as squirrels, were often stuffed (occasionally with wild rice in the Midwest) and used as toys. Several tiny birch bark cones or funnels were usually included among cradleboard toys in the Eastern Woodlands. One or more of them was filled with hard maple sugar and hung so that the baby could reach it and put the cone into his mouth and get a little of the sweet taste. Sometimes animal skins were used in place of the birch bark container. Infants of the Huron tribe in the East often had their cradleboards decorated with strings of wampum beads and little paintings.³

Once the child left the cradleboard, he was often amused by toy ducks, floating on some body of still water. The toys were made, usually in groups of five among

the Chippewa, from the outer covering of cat-tail rushes. By blowing across the smooth water, the child agitated the ducks which moved in a life-like manner. The vivid imagination of childhood was all too soon lost but while still very active, sticks and rocks, wisps of cloth, and bits of this and that became treasured playthings. Indian children enjoyed a wide variety of playthings, limited only by invention and the materials with which to fashion them.

Perhaps the most widely diffused of all toys was the top. Most Indian children played with tops during the cold winter days when rivers and lakes were frozen. Tops were constructed of wood, horn, stone, bone, ivory, or clay. However, the Chippewa on the Apostle Islands off the Wisconsin shoreline in Lake Michigan used acorns and nuts. Quinault boys on the northwest coast of Washington played with tops made of skunk cabbage sections about two inches long, thrust through with a salmonberry spike. Most of the tops measured approximately two and a half inches in length, tapering from a diameter of an inch and a half down to a point at the base. Sometimes tops were painted. Another form was disc-shaped with a diameter of about four inches. This type was set in motion by twirling it between the palms of the hand. Some tops used string of sinew or buckskin and were kept moving by utilizing a whip. Each top owner wanted his to spin the longest or farthest and so Indian children frequently played and practiced with their tops. Sometimes Chippewas played with oval stone-like tops, whipping them across the winter ice with force enough to upset another's stone and thereby claim victory. The southern Okanagan of the inland Pacific Northwest had a competition in which an attempt was made to split another's wood or bone top.

Sledding was enjoyed by children in many parts of the continent. Blackfoot and Nez Perce boys and girls coasted down hills on flexible buffalo toboggans or deerhide (hair side next to the snow). These were fashioned with an upturned front section which turned aside the snow as they coasted along. San Poil and Nespelem youngsters of the Plateau culture area would occasionally substitute pine boughs for the hide. Chippewas, too, had fun in the snow with a sled that sounds much like a forerunner of skis. Boys, and girls who were frequently as proficient in outdoor sports as boys, liked to swoop down hillsides erect. To do this a strip of wood or slippery elm bark was strapped to the feet. This runner was about three feet long and four inches in width, curving upward at the forward end. There a thong was attached, to be held in the hand, both for guiding one's direction and for stability. A long stick to maintain one's balance was permissible but frowned upon by the participants as the youngsters chose the steepest hills, thereby acquiring a reputation for bravery and self control.

On the Plains where wood was not plentiful another innovation was found. There boys used sleds of bison ribs. Five to ten bones were separated from the backbone but re-assembled in the same order and tied tightly together at the ends with rags, sinew, or rawhide. Sometimes a piece of buffalo skin was used for a seat and a rope of rawhide attached to the front end. Before his first run, upon completing construction, the owner towed his sled about in the snow to coat the runners and assure himself a thrilling ride.

On the Plains and in the adjacent woodland areas children often made toy figures where deposits of riverbank clay were available. This childhood custom of modeling forms from wet clay was so prevalent that a clan of the Hidatsa tribe has derived its

name from this practice.⁴ Blocks for building villages were produced as were figures of horses, dogs, buffalo, and men. Children of the North Woods often selected the wolverine for reproducing in clay form. Teton Sioux children, especially, fashioned animals with amazing fidelity.⁵ The horse, of vital importance to Indians of the Plains, appeared repeatedly, sometimes in lengths of twelve inches. While the clay was still soft, young boys would place sticks in the end of each leg. After a time in the sun for drying, the horses could stand more readily on the ground and be placed in various positions in the child's game of pretend.

Widespread among Indian children were tops known by such names as bull-roarer, whizzer, and buzzer. Although the bull-roarer or whizzer was used as a toy among most western Indian tribes, it appeared in the Southwest for ceremonial purposes. Slight variations occurred in the mode of operation and construction. Sometimes made of a flat piece of bone, pottery, or gourd, a six-inch piece of wood was more common. This was occasionally highly decorated with paint, notched at the edges and had a length of sinew or buckskin attached to it. Held in one hand, the cord was spun around in the air quite rapidly and produced a roaring sound. Some tribes attached the thong to a long stick and spun it around. The hummer or buzzer likewise produced noise as a piece of bone or wood was whirled in the air. This object had cords on both sides, passing through holes in the object, and by alternately twisting the cords as the operator rapidly slackened and drew taut the strings, a humming sound was made.

One toy, in the category of those that were propelled, was a type of bean shooter which has been found only in the Southwest and on the Northwest Coast. The Hopi employed a piece of cane with a spring, consisting of a bent piece of wood, the ends of which are secured in holes cut into the cane. The Kwakiutl of the Northwest Coast had a figure-four dart shooter which was a small stick placed across the top of pliant side pieces and shot by pressing on the trigger piece which was horizontal to the figure-four. Frequently used by sick children, small sticks were shot in different directions to chase away the spirit supposed to be causing the sickness.

Quinault children of the Northwest also used a sling-propellant and stone thrower. The sling was made of a thong or a strip of cedar or willow bark. The thrower consisted of a curved stick about a foot and a half in length, split with the inside cut away to form a slot. Stones were wedged into the slot and were discharged by throwing overhand. In the interior of Washington State the southern Okanagon considered the sling a child's toy, not a weapon. It consisted of a piece of leather about five inches in length by two and one half inches in width, tapering at the ends, to which braided hemp cords were tied. One cord ended in a loop which was slipped over the forefinger, the other to be held between the thumb and forefinger. The knot was released when the missile was thrown.

As with their elders, horses played a significant role in the life of children who lived on the Plains. A child's association with these animals began at a tender age and increased as he matured. Hobby horses were the first favorite with the very young of the Blackfoot nation. To make these toys, a rather heavy tree trunk with a double bend was selected. With the bark peeled off, the thicker, lower end of the trunk was placed in the ground so that the bends would be approximately thirty inches above the ground. A carved horse head was attached occasionally to give a more realistic appearance which a bundle of weeds or a hank of horse hair tied to the rear

completed. When boys reached about eight years of age they started to fashion their own hobby horses from willow branches. The end of a piece was split down the middle, half of which was turned upward to form the neck and head; the remaining half formed the forelegs. The other end of the twig was similarly split, one half being made into the legs and the other half, the tail. Arapaho girls duplicated these toys but used two pliable sticks which they had bent into semi-circles and fastened to a straight piece of willow, thus forming the four legs and the back of the horse. Another willow twig was fashioned for the head and a bunch of weeds made the tail. Occasionally a miniature travois or a piece of hide to make a saddle was added.

Native plants often did service as toys for the young. Indian children living in the forest areas of the Midwest made whistles for themselves of wild onion stems. Willow was used for this same purpose in the Plateau area between the Rockies and the Cascades. Leaves of the pitcher plant were called "frog leggings"⁶ by children and filled with ripe berries or sand for their world of play. Pine needles, bent and inserted in the socket of the needle at its base, formed a loop that resembled the frame of miniature snow shoes. When these circles were interlaced, a necklace chain was formed. Bright red berries, strung on a cord of nettle fiber, also served as a necklace in the enchanted world of childhood.

The competitive spirit was strong in many tribes and like little boys everywhere, Indian boys enjoyed throwing objects to see how far they would go. Youngsters on the Plains have special throwing sticks which they made for this particular pleasure. Long, slender, springy sticks were selected and tipped with buffalo horn. Thrown forward by one end, the stick turned over and over in the air, striking the ground and bouncing up again. Again it revolved several times and hitting the ground once more, repeated the process, thus advancing by leaps for a considerable distance. Another version consisted of a piece of buffalo rib in which holes had been drilled and feathers inserted so the toy would fly evenly. With an underhand throw the implement was set sailing horizontally above the ground surface. When the piece contacted the ground on its convex side, it ricocheted and advanced. This type of play was primarily a winter amusement.

Stilts appear less frequently as toys but are reported in areas great distances apart. The Maya of Central America used them in dancing. Boys of the Hopi and Zuni tribes utilized cottonwood poles for walking above the ground. Shoshonean tribes are also known to have had them. Little Chippewa children used short sticks, about three feet in length, as "arm stilts" which gave the appearance of being four legged. The boys imitated the actions of deer, striking out with their "legs" at those who happened to be nearby.

Swinging was a popular diversion with children. The southern Okanagon made use of swings during the summer months; Twana children in western Washington State also had swings or swinging ropes. The Quinault of the Northwest had a somewhat different type of swing. Long forked poles were lashed together near the top with another pole placed in the forks, making a cross bar. A person sat upon a braided willow bark rope and was pushed by another. Singing was a part of this activity.

Adults of some tribes supplied children with certain toys to assist in the promulgation of religious practices and concepts. Such was the role of the kachina doll of the Southwest. The kachina cult has as its core the worship of supernaturals through im-

personation. At religious ceremonies masked dancers represent and impersonate a multitude of spirits; the wooden kachina dolls represent the masked dancers. Although the religious cult among the Zuni and Hopi reaches far back into history, present evidence, admittedly incomplete, suggests that production of the dolls began less than one hundred years ago.⁷

The figures are made of the soft, white cottonwood root and have facial features attached by glue or dowels. Most are from eight to ten inches tall, although a few might measure as much as two and one half feet in height or as small as two or four inches tall. Masks are painted on the figure, formerly done in mineral colors, after a coat of white clay has been applied. Today water colors or poster paints decorate the doll. Dolls from Zuni villages usually have moveable arms and garments of cloth whereas the Hopi paint these on the doll. Kachinas are rarely made at other villages.⁸ Young children frequently received a doll from masked dancers during religious ceremonies and perhaps a present of fruit and nuts as well. Despite the fact that the kachinas were not made to be used as playthings, little girls often regarded them and used them as baby dolls.

Little girls of the Twana tribe of western Washington (sometimes called Skykomish) wrapped a live newt or lizard in moss and cedar bark, treating it as a baby. This was not considered strictly play, however, but a type of training for acquiring future spirit power.

Toys were occasionally presented for esthetic motives. Many Eskimo dolls were actually works of art and mechanical ingenuity, intended to attract the eye of those who appreciated such things. One, a seated man dressed in buckskins, held in his right hand a stick. In his extended left hand was a drum, and by pressing his whale-bone arms, he could be made to beat the drum. The height of the sitting figure was just under twelve inches and was made from one piece of wood, a knot with two branches making the legs. Some tribes of the Southwest had mechanical birds.

Made to assist the child in assuming an adult role were replicas of articles used by elders as they went about daily tasks. Prominent were the play bow and arrow, which many toddlers received as soon as they could hold them. So very much in later years depended on the individual's skill in their use that association with them began early in life. At first, little boys used only blunt arrows and part of the daily routine was practice in shooting. By six years of age Kutenai boys of the Intermontane Northwest were expected to kill birds regularly and furnish part of their food. Parents were not motivated by economic pressures but rather believed this to be an educational and disciplinary action. Upon reaching ten years of age, boys of this tribe made their own bows and could furnish bison calves for the family table. Miniature salmon and bird darts as well as leister prongs helped train Eskimo boys for the duties of adulthood.

Youngsters living near oceans, rivers, and lakes numbered canoe models among their favorite toys. In California, Yurok boys of four and five years of age played with pine bark vessels about a foot long. However, cautious parents forbade their use in rivers or creeks, permitting them to be floated only in pools the children scraped out of the sand in a stream. Klallam and Coeur d'Alene children in the Northwest also treasured the miniature canoes made for them by elders.

Eskimo boys had several types of canoes which included kyaks and umiaks. Some

were fitted with tiny paddles and the gear for a sea hunt. Eskimo children, in general, had a greater variety of toys than children of any other native peoples. In addition to the items already mentioned there were little drums, snow shovels, buckets, sleds, hunting outfits, dishes, and lamps.

As is true of little girls worldwide, Indian children also relished playing house. Its educational benefits were long lasting, for many of the activities of their pretend world became real in a few short years. At play, little girls learned the basic facts of baby care, housekeeping, preparations for moving and setting up camp, crafts, and even cooking. On the Plains Arapaho girls might have a play tipi two or three feet high which permitted playmates to be inside it as well as themselves. Sometimes these were quite elaborate, being beaded and having poles of cedar. When a little older, the girls might sew gopher or ground squirrel skins together for tipi covers or for use as beds or floor mats.

Young girls of the southern Okanagon built salmon traps and weirs as part of their play, keeping house. Chippewa girls often cut large lichens growing flat on tree trunks to decorate the walls of their playhouses in much the same way as their mothers placed yarn bags along the walls of the family's wigwam. Mothers also showed their daughters how to take bark from small birch-bark trees to make rolls for wigwam covers. Birch bark utensils were made in imitation of those used by adults of the tribe.

In Central British Columbia the Thompson and Lillooet people fashioned houses for dolls, frequently imbricated with designs representing house beams and furnished with miniature painted and carved ladders. When a replica of an "underground" type of house was constructed, only that part which showed above the surface was made. Further south in the Intermontane Plateau, San Poil and Nespelem children drew outline pictures in the sand for their doll houses. Miniature utensils and animals were cut from pieces of riverbank clay and placed in and about the doll house. Unfortunately, few considered these playthings worthy enough to save for the next day's play.

On the Northwest Coast shells represented doll people—scallops stood for those people of the Interior and mussels for those who lived on the Coast. A rough and dirty shell was a bear and a slender one with a pointed end was a dog. A round shell holding bits of seaweed was, to the Indian children, the serving dish at a feast. A large mussel shell served nicely as a canoe, transporting the shell family over the water.

Dolls of all levels of sophistication aided significantly in teaching responsibilities for later life. Very young Chippewa girls were delighted with pine needle dolls. These were made from tufts of Norway pine, trimmed at various lengths to suggest the bottom of a dress and arms, or a shawl over the shoulders. A bit of wood was left to take the place of a head. However, no attempt was made to denote facial features. Densmore states "it appears in this stage of primitive art it was not necessary to show details of an object . . . the articles represented nature without being a close imitation of nature."⁹ These pine needle dolls were placed on a large piece of birch bark, or later, a tin pan, which was rotated smoothly, giving the figures the appearance of dancing. Dolls of this type were also made from broad tree leaves which were fastened in place with little splinters of wood. Occasionally, a collar or shawl of birch bark was added to the costuming. Bulrushes sometimes substituted for leaves.

As the youngsters became a little older, this type of doll was not satisfactory as they desired more realistic playthings. Flat male and female figures were cut from

the stiff inner bark of the slippery elm or from that portion of bulrush root that is below water. When the latter material was used, it first had to be partly dried before it was fashioned into a figure. When completely dried it could be handled without breaking. Again, no attempt was made to denote facial features. The flat figures were fairly durable and easily packed, for the child had to keep possession of her own toys as the people moved from camp to camp. Dolls made from grass were occasionally given to little Chippewa girls as a reward for work well done, in place of praise which they were seldom given. The Quinault also made a primitive type of doll of a bundle of cedar bark. It was tied tightly just above the end of the folded portion to form the head and neck. A stick placed crossways formed the arms. The waist was indicated by another tie below which was added shreds of bark for a skirt.

Blackfoot grandmothers often made dolls for little girls in the family, selecting a section of birch perhaps a foot long and four inches in diameter. They would cut a groove about a third of the way from one end—the doll's shoulders. A crude, knob-like head was whittled. Small holes denoted the facial features. The doll had no ears, legs, or hair. Below the shoulders the body was merely a length of wood. The young child dressed the doll by wrapping a piece of buckskin, or trade cloth, around the cylinder. Older girls were not so easily satisfied and wanted dolls with arms, legs, more realistic heads, hair, and pretty clothes. Little girls everywhere have a way of obtaining those things they desire and thus the older group soon played happily with well-proportioned dolls having skin or cloth heads, human or horse hair, facial features of thread, trade beads, or paint, and garments like those worn by the tribe. Often little girls received their first lessons in beadwork by sewing beads on a doll's dress. On the Plains, girls of six or seven learned to sew clothes for their dolls and frequently made tiny moccasins from dressed antelope skins for their "babies," often a puppy.

Flathead women especially were clever at making lovely dolls.¹⁰ They took great pains to paint the face appropriately and they made exquisite buckskin clothing. It was not unusual when a Flathead girl married to take the dolls with her into the lodge and treasure them for life. As a contrast, at the onset of puberty, a girl of the Nootkan tribes of the Northwest Coast gave away all toys. Young girls of the San Poil and Nespelem tribes of the Plateau region played with dolls which they made themselves. A stick covered with grass and then buckskin formed the body. The head was made by wrapping a pebble in buckskin and lashing it to the doll's body or by modeling soft clay and securing it to the figure. Children in the vicinity of Lake Okanogan, Washington, are reported to have had dolls of stone, some of which were really gold nuggets. One child in particular traded her doll of some six inches in length for a white linen handkerchief, never realizing its value.¹¹

Among the Kutenai, as soon as a toddler could walk, she was given a doll and a toy cradleboard. Her mother went to considerable lengths to see that her play was realistic and encouraged the child to play with the doll all day long. The little one would understand some of the basic facts of child care and be of assistance to the mother when the next baby came along. Kutenai parents encouraged the educational progress of their children by giving them lavish praise for their accomplishments.

In all times and all places toys have served similar purposes for children. Some are utilized to instruct and some to amuse. On occasion, a gift of a toy is presented to a child solely to be admired. Toys may serve as vehicles to clarify religious concepts.

Others may have the function of a prop, to strengthen the body and inure it to pain and hardship. However, the children viewed a great number of toys simply as fun.

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The Rocks and Structure of the White Pass Area, Washington

Introduction

The White Pass region (Figs. 1 and 2) of the Cascade Mountains in Washington state lies at the northern edge of the Goat Rocks Wild Area. Comparatively little is known of the geology of this area. This paper presents field and petrographic data from the region along the White Pass highway. This work is part of a larger study to work out the gross structure and map the major rock types in the central and northern part of the Goat Rocks-White Pass area. Additional field work will be needed to establish the regional significance of the information given here.

Summary of the Rocks of the White Pass Area

Pre-Tertiary Rocks

Limestone

Fragments of gray limestone (oöpsparite), ranging in length from several inches to two feet, are found between Miriam and Hell Creeks on the west side of the North Fork of the Tieton River. The limestone fragments are found mixed with blocks of Twin Peaks Diorite Porphyry and graywacke of the Russell Ranch Formation at the 4000-ft level at the base of a large talus slope.

Oolites in the limestone contain foraminifera (Fig. 3) that have been identified by Lee Holcomb of the Shell Oil Company as "definitely post-Mississippian and pre-Triassic and probably Permian" (Ellingson, 1969).

The stratigraphic relations between this rock and other pre-Tertiary rocks are unknown.

Indian Creek Amphibolite

The Indian Creek Amphibolite, mapped to this time as a Tertiary intrusion, crops out north of the outlet of Clear Lake forming Kamiakan Butte, and crops out along the east side of Indian Creek at the west end of Russell Ridge.

Approximately 80 percent of this body is amphibolite. Quartz diorite pegmatite dikes up to four in wide intrude the amphibolite on Kamiakan Butte and along the Clear Lake fault zone. The amphibolite and pegmatite have been intensely sheared and mixed along the Clear Lake fault zone forming cataclastic orthogneiss and mylonite (Figs. 4 and 5).

Preliminary study of the amphibolite shows that it was metamorphosed at least twice. The grade of the first event is difficult to determine. The green to light brown hornblende, which has been partially altered to blue-green hornblende and actinolite of the greenschist facies, and the alteration of intermediate plagioclase to clinozoisite

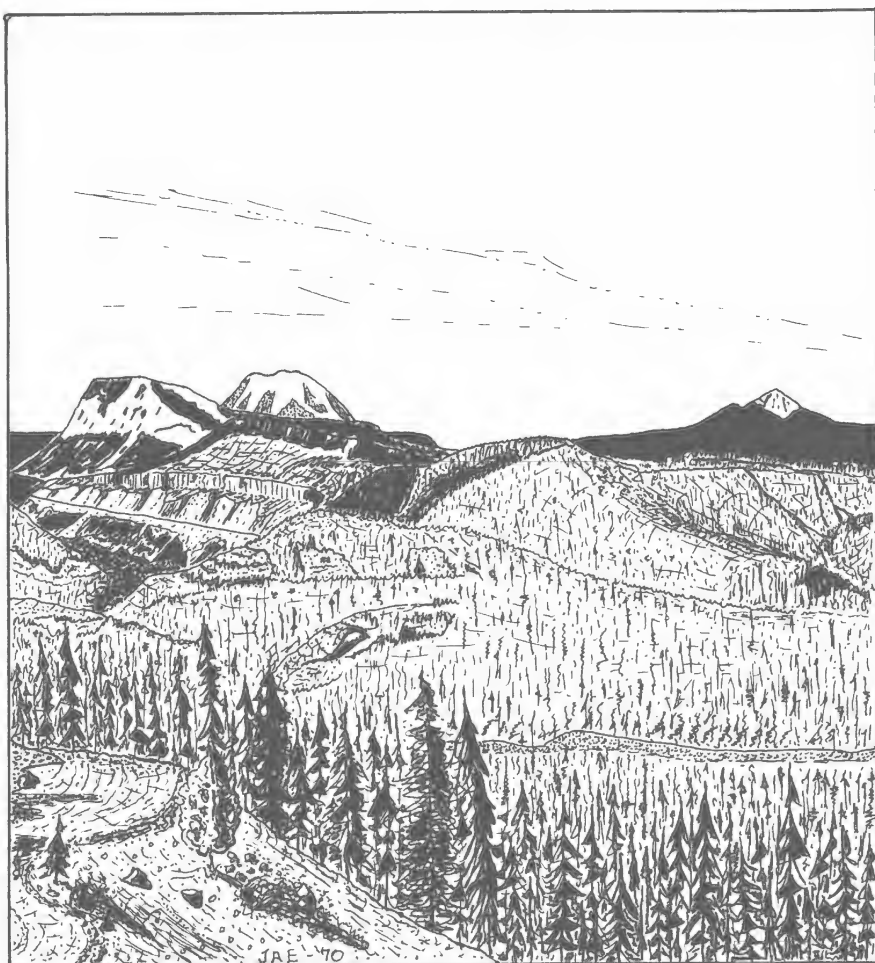


Figure 1. Index sketch of the eastern White Pass region looking northwest across the Cascade Crest. On the right is the Tumac Plateau, Tumac Mt., and Indian Creek. In the middle distance is Kamiakan Butte. To the left of Mt. Rainier is Spiral Butte, White Pass highway, and Clear Creek.

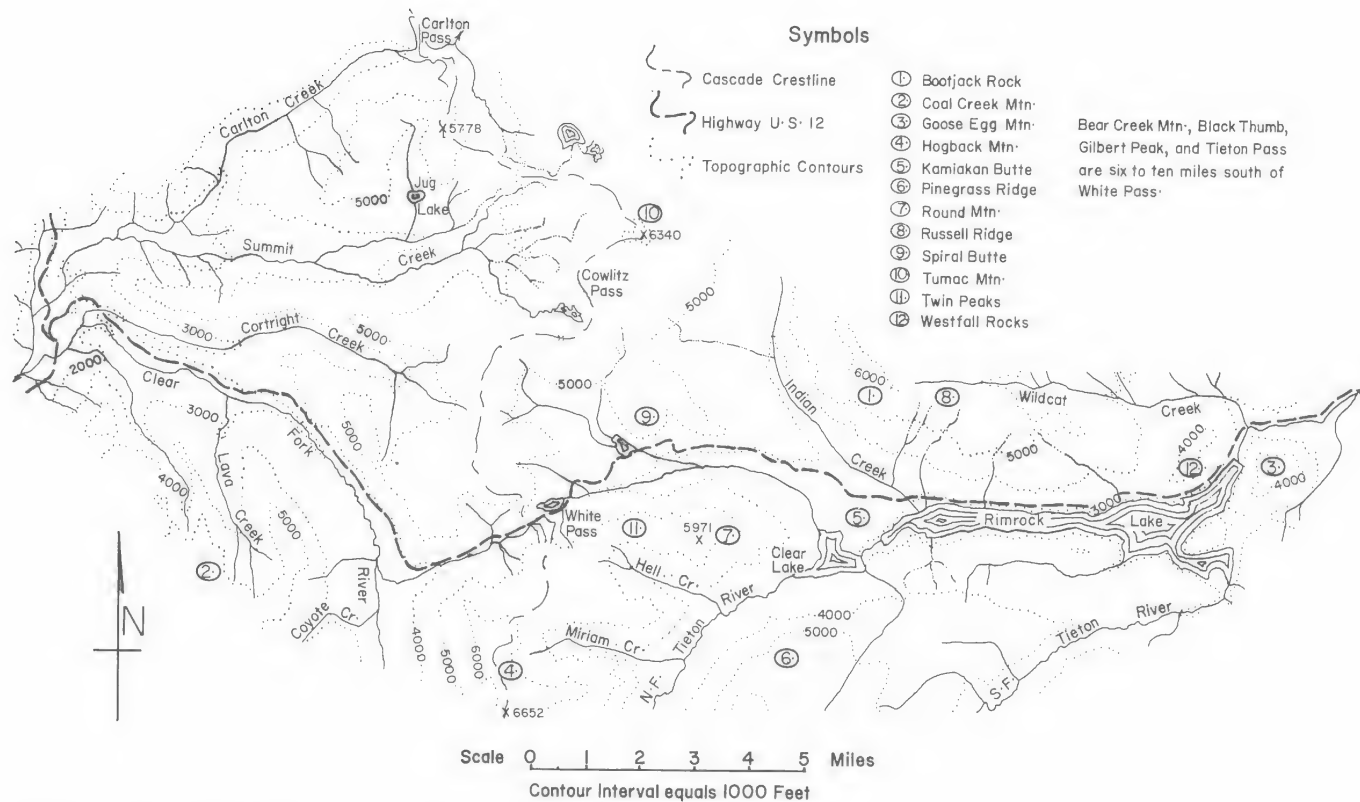


Figure 2. Topographic and location map of the White Pass Region.

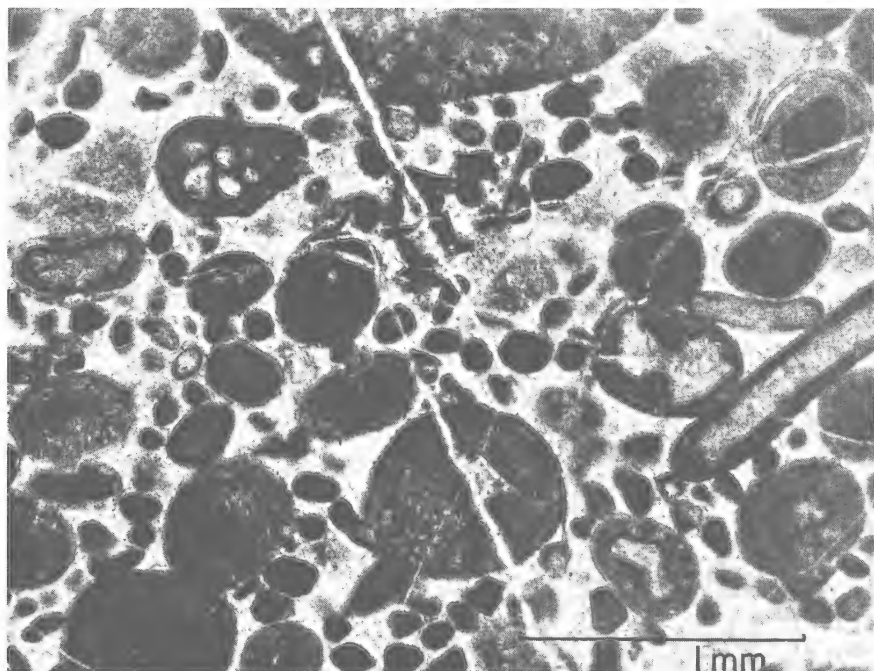


Figure 3. Photomicrograph of the oopelsparite. Oolites, foraminifera, and fecal pellets are embedded in a sparry calcite matrix.

suggest that the original minerals formed under amphibolite facies conditions.

The grade of the second event, as indicated by the coexistence of actinolite and blue-green hornblende and the coexistence of clinozoisite and andesine, was high-temperature greenschist facies (Winkler, 1967). The presence of cummingtonite indicates that locally the rocks developed pressures and temperatures of the amphibolite facies.

On the eastern side of Kamiakan Butte where shearing was not so intense, pegmatite dikes and amphibolite are distinct lithologies and have the same metamorphic grade. The dikes contain andesine (An_{36}), hornblende, epidote, and quartz. The hornblende, where it is relatively unaltered, has strong blue-green pleochroism.

Russell Ranch Formation

The Russell Ranch Formation is a heterogeneous sequence of submature feldspathic subgraywacke and thin lenses and layers of argillite, carbonaceous siltstone, conglomerate, and basalt. These rocks crop out at Rimrock Lake, at lower elevations along the North and South Forks of the Tieton River, and at White Pass.

Deformation was so strong that stratification is almost completely lacking in the graywacke. Where stratification is present in the more heterogeneous parts of the formation, attitudes change radically over short distances.

The base of the Russell Ranch Formation is not exposed in this area. Altered

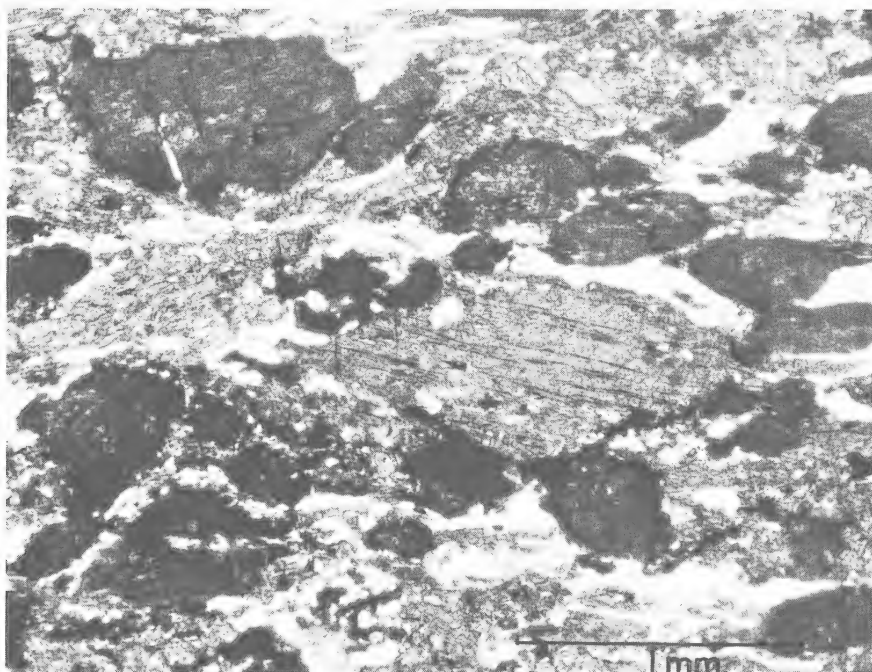


Figure 4. Photomicrograph of the Indian Creek Amphibolite. The minerals shown include quartz, blue-green hornblende, clinozoisite, and leucoxene. Plane light.

pillow(?) basalt is in fault contact with Indian Creek Amphibolite on the east side of Kamiakan Butte. This basalt may mark the lowest exposed stratigraphic unit of the Russell Ranch Formation on the basis of outcrop elevations and map patterns. The contact between the Russell Ranch Formation and all younger rocks is, from place to place, an angular unconformity, a fault, or an intrusive contact.

Tertiary Rocks

Tertiary lavas and volcanic clastic rocks are the most abundant rocks on the flanks of the Cascades. They are almost totally absent from the center of the range in the White Pass area. The Tertiary rocks include the Ohanapecosh Formation to the west, the Fife Peak Formation to the east, plutons to the east and west of the Cascade Crest, and the upper Miocene Yakima Basalt to the east and southeast. The Yakima Basalt crops out on Bethel Ridge and Divide Ridge but does not extend into the map area (Swanson, 1967).

Ohanapecosh Formation

The Ohanapecosh Formation of Eocene age is mapped for this report as an undifferentiated unit containing volcanic clastic rocks, former lava flows, and sandstone with coal beds (Fiske, Hopson, and Waters, 1963). The formation can be traced continuously from the southeastern corner of Mount Rainier National Park along the



Figure 5. Photomicrograph of the Indian Creek cataclastic orthogneiss. Note the deformation of individual plagioclase crystals. Crossed nicols.

eastern side of Coal Creek Mountain to Old Snowy Mountain in the Goat Rocks Wild Area (Ellingson, 1968). These rocks form a homocline which strikes to the north-northwest and dips 28° to 65° to the west.

The top of the formation lies out of the map area to the west. A basal conglomerate marks the base of the Ohanapecosh Formation in Cortright Creek. In most places, however, the Clear Fork fault zone and the Jug Lake pluton mark the base of the formation.

In Summit Creek, near the base of the formation, thin carbonaceous siltstone and coal layers are part of a 2000-ft sequence of massive cross-bedded arkosic sandstone and mudstone of middle Eocene age (Ellingson, 1959).

Fifes Peak Formation

Upper Oligocene to lower Miocene ash flows and the Fifes Peak Formation of Miocene age are described by Swanson (1966) east of the mouth of Wildcat Creek along the Tieton River. Most rocks of the Fifes Peak Formation are andesite flows, rhyolite ash flows, slurry-floods, tuff, and pumice floods.

Small isolated outcrops of rhyolitic ash and breccia, which may be part of the Fifes Peak Formation, crop out on the east side of Round Mountain, at Bootjack Rock at the west end of Russell Ridge, and on the west bank of Indian Creek three and one-half miles upstream from Rimrock Lake.

Plutonic Rocks

The diorite to quartz diorite plutons in the area are the Jug Lake pluton on the west side of the Cascade Crest and the Twin Peaks pluton three miles southeast of White Pass. Numerous dike and sills are associated with each pluton.

The composition and complex history of the minerals indicated by texture, zoning, and alteration strongly suggest that these plutons belong genetically and in time with other Miocene plutons of the Cascade Mountains (cf. summary Fiske, Hopson, and Waters, 1963). The middle to late Tertiary age of these plutons is indicated by their cross-cutting relations with the folded Ohanapecosh and Fifes Peak Formations and their nonconformable relations with Quaternary lavas.

Discordant andesite porphyry and basalt porphyry hypabyssal bodies form Westfall Rocks, Goose Egg Mountain, Chimney Peaks, and Kloochman Rock at the outlet of Rimrock Lake (New, 1940). New proves that these bodies are intrusive into the "Lower Keechelus" and suspects them of being conduits for the "Upper Keechelus" (Fifes Peak).

Quaternary Volcanic Rocks

Volcanic rocks from five separate vents crop out on the ridges and form intercanion flows in the White Pass area. The following descriptions of these flows are listed in order of decreasing age (Ellingson, 1968).

Tieton Andesite

The Tieton Andesite (Smith, 1903) is exposed in the ski area on the south side of White Pass, 500 ft up-slope from the highway. Pinegrass Ridge, south of Rimrock Lake, is capped with Tieton Andesite. Becraft (1950) studied these lavas where they become intracanyon flows in the unglaciated part of the Tieton River valley east of Westfall Rocks.

TABLE 1. Chemical analyses of andesite from Mt. Baker and Mt. Rainier (Coombs, 1939, p. 1506) and andesite and basalt from the White Pass area. Analyst for 4, 5, and 6: Andrew S. McCreath and Son, Inc.

Oxides	1.	2.	3.	4.	5.	6.
SiO ₂	60.95	60.53	61.50	60.05	58.56	50.51
Al ₂ O ₃	16.87	17.01	17.14	17.23	16.92	18.28
Fe ₂ O ₃	1.58	2.12	1.55	1.86	1.73	2.10
FeO	3.52	3.58	3.85	3.92	5.38	7.09
MgO	2.75	3.47	2.96	2.82	3.62	6.67
CaO	5.20	5.79	5.80	4.62	5.44	8.36
Na ₂ O	4.48	4.01	4.11	4.10	3.88	3.15
K ₂ O	2.08	1.58	1.65	2.59	2.39	0.63
H ₂ O ⁺	0.97	0.25	0.20	1.28	0.37	1.04
H ₂ O ⁻	0.16	0.12	0.04	0.13	0.28	0.16
TiO ₂	0.90	0.95	0.91	1.25	1.36	1.39
P ₂ O ₅	0.27	0.26	0.25	0.24	0.28	0.21
MnO ₂	0.10	0.10	0.10	---	---	---
	99.83%	99.77%	100.06%	100.09%	100.21%	99.59%

1. Andesite from Austin Lake, Mt. Baker.
2. Andesite from Burroughs Mountain, Mt. Rainier.
3. Andesite from the summit of Mt. Rainier at Register Rock.
4. Sp. #15-66. Tieton Andesite from one mi east of the upper end of the White Pass chair lift.
5. Sp. #43-66. Tieton Andesite from the summit of Bear Creek Mountain.
6. Sp. #45-67. Hogback Mountain Olivine Basalt from the summit of Hogback Mountain.

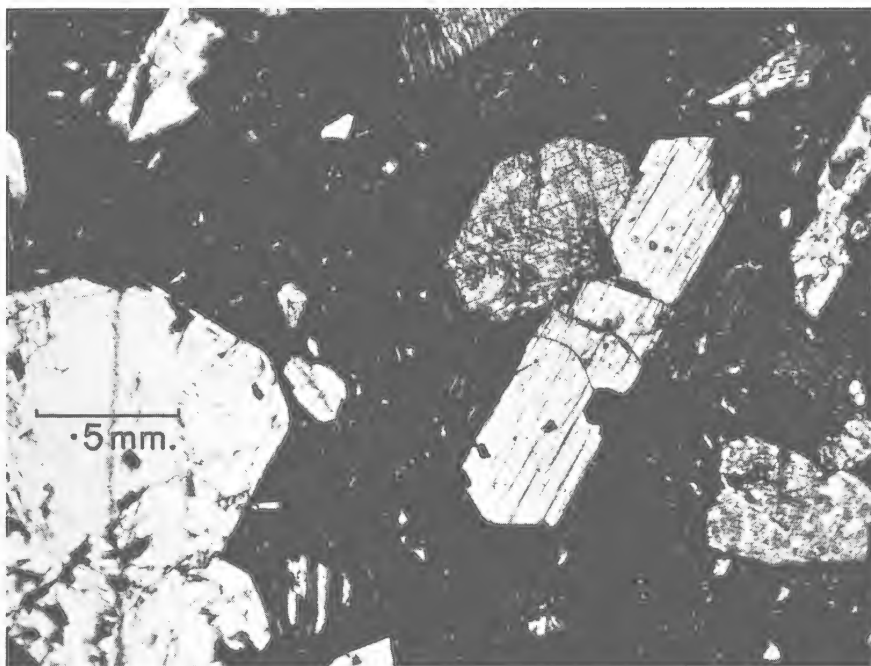


Figure 6. Photomicrograph of the Tieton Andesite. Hypersthene, augite, and plagioclase are embedded in a glassy microlitic groundmass. Crossed nicols.

The Tieton flows are porphyritic pyroxene andesite, very similar to the andesite of the large volcanoes in the north Cascades (Fig. 6 and Tables 1 and 2). The source for the Tieton Andesite is marked by Black Thumb and Gilbert Peak, both of which are part of a volcanic neck at the site of a large Pliocene to lower Pleistocene volcano in the southern part of the Goat Rocks Wild Area (Ellingson, 1969).

Spiral Butte Andesite

Spiral Butte Andesite crops out on both sides of the White Pass highway from the summit to three miles east of Spiral Butte and on the west and northwest of Tumac Plateau. This dense, light gray lava has strong linear flow-banding giving the rock a characteristic platy rock cleavage. The vent for this lava was Spiral Butte, a flat-topped cone located just north of the highway two and one-half miles east of the summit.

Hogback Mountain Olivine Basalt

Hogback Mountain Olivine Basalt crops out along the ridge south of White Pass and on Hogback Mountain in a series of thin, highly vesicular flows. Olivine phenocrysts and smaller augite phenocrysts are conspicuous in most flows (Figs. 7 and 8). Chemically, the rock is a high alumina olivine basalt (Tables 1 and 2.)

The vent for the Hogback Mountain Olivine Basalt is marked by a volcanic neck 0.5 mi south of Hogback Mountain. The flows apparently ponded in a mile-wide

TABLE 2. Water-free analyses and CIPW norms of rocks from the White Pass area. All analyses and norms recalculated to 100%.

Oxides	4.	5.	6.
SiO ₂	60.85	58.82	51.33
Al ₂ O ₃	17.45	16.99	18.58
Fe ₂ O ₃	1.89	1.74	2.14
FeO	3.98	5.40	7.21
MgO	2.86	3.63	6.78
CaO	4.68	5.47	8.49
Na ₂ O	4.15	3.90	3.20
K ₂ O	2.63	2.40	0.64
TiO ₂	1.27	1.37	1.42
P ₂ O ₅	0.24	0.28	0.21
Norms (wt. %)			
Q	10.93	8.32	-----
Or	15.59	14.42	3.32
Ab	35.14	32.92	27.10
An	21.43	21.63	34.28
Ol		-----	0.84
			0.41
Di		0.46	2.88
		0.30	1.79
		0.13	0.91
Hy		6.91	14.52
		3.56	7.88
		2.43	2.73
		2.78	3.00
		0.34	0.34
Normative plagioclase	An ₃₈	An ₄₀	An ₅₅

crater forming a sequence of thin horizontal basalts 35 to 40 flows deep. A valley, cut into the Tieton and Spiral Butte lavas, guided the olivine basalt for nine miles north and west of White Pass to a position near the junction of Lava Creek and the Clear Fork River.

Tumac Mountain Olivine Basalt

Tumac Mountain Olivine Basalt and the Tumac Mountain cinder cone are mapped and described by Abbott (1951, 1953). These lavas form the Tumac Plateau along the Cascade Crest between Carlton Pass and White Pass and form intracanyon flows in Summit and Indian Creeks.

Clear Fork Dacite

The Clear Fork flow is confined to the glaciated valley of the Clear Fork of the Cowlitz River. The flow forms a broad bench in the valley from Coyote Creek to near the mouth of the Clear Fork—a distance of about eight miles.

The vent for this lava is on the ridge dividing Lava Creek from Coyote Creek on the east side of Coal Creek Mountain. The very fine texture of this rock makes petrographic study of it difficult. Larger grains of quartz in the pilotaxitic groundmass of

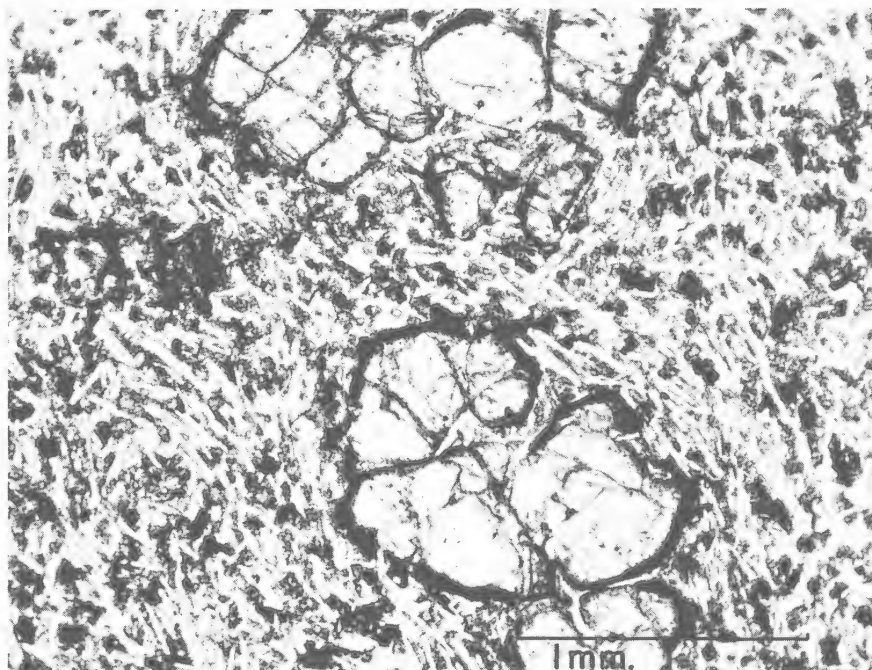


Figure 7. Photomicrograph of the Hogback Mountain Olivine Basalt. The olivine with rims of iddingsite is in a pilotaxitic groundmass of grains of augite and laths of plagioclase. Plane light.

intermediate plagioclase suggest that the rock is dacite. Long slender columnar joints are exposed where the flow has been eroded by the Clear Fork River and by other creeks. At the observation point on the White Pass highway, continuous joint-columns about 200 ft long extend from the top to the bottom of the flow.

The unusual length of these columns suggests that the lava ponded against something which kept it from continuing down the valley. The obstruction may have been the Clear Fork fault scarp.

Structural Geology

The White Pass region is nearly ideal for observing the Tertiary geologic history of the Cascades as outlined by Mackin and Cary (1965). The history of the pre-Tertiary rocks stands in marked contrast to Tertiary history. There is no fixed stratigraphic succession which can be used to work out folds and faults in the Russell Ranch Formation. Contacts of the main pre-Tertiary units are sheared wherever exposed making structural trends very difficult if not impossible to follow. Besides, the ever-present trinity—slope, talus, brush—plague the geologist in this area as in other parts of the glaciated Cascades below timberline.

Structure of the Pre-Tertiary Rocks

The shearing of the graywacke in the Russell Ranch Formation has destroyed all



Figure 8. Photomicrograph of a specimen of the Hogback Mountain Olivine Basalt from the volcanic neck just south of Hogback Mountain. An olivine phenocryst and microphenocrysts of labradorite are in a microcrystalline groundmass of plagioclase, augite, and magnetite. Crossed nicols.

traceable folds. Where the Russell Ranch Formation is more heterogeneous along Rimrock Lake, bands and lenses of siltstone and carbonaceous siltstone are folded into irregular antiforms and synforms. The folds are characterized by rapid variation in bed thickness due to shearing. The strikes of the fold axes range between $N 30^{\circ} W$ and $N 30^{\circ} E$.

The Indian Creek Amphibolite is a lens-shaped body bounded on the east and west by fault zones. The following evidence indicates that the amphibolite was emplaced as a solid by intense tectonic transport.

1. There is a marked difference in metamorphic grade across the fault zones separating the amphibolite from the Russell Ranch Formation.
2. Blocks of Russell Ranch Formation caught in the cataclastic orthogneiss along fault zones show no sign of thermal metamorphism.
3. The cataclastic orthogneiss is found only along the marginal faults and the foliation in the orthogneiss parallels the strike of the faults.
4. The pegmatite dikes are confined to the amphibolite.

Helicitic amphiboles and rodding structures in the orthogneiss show the effects of shearing during metamorphism. Mylonite, broken plagioclase crystals (Fig. 5), and

undulatory extinction in composite quartz grains show that intense shearing along the Clear Lake fault zone followed greenschist facies metamorphism.

Lipman (1964) suggests that pegmatite dikes, such as those in the Indian Creek Amphibolite, form from interstitial silicate magma generated during emplacement of the body. The quartz-rich mylonite, rodding structure, quartz diorite composition of the bands in the orthogneiss, and greenschist facies metamorphism of the dikes suggest that the intrusion of the pegmatite dikes took place prior to, and possibly during, the tectonic transport of the amphibolite to its present structural position in the Russell Ranch Formation.

History of the Pre-Tertiary Rocks

The limestone fragments of Pennsylvanian to Permian age are cut by a fine network of sparry calcite veins. These rocks are otherwise completely undeformed. The oolites, pellets, interclasts, and fossil fragments are not deformed or oriented (Fig 3). Weathering of the surfaces of the blocks destroyed any slickensides which may have been present. This lack of deformation suggests that the limestone is younger than the deformed Indian Creek Amphibolite and the Russell Ranch Formation. If this is the case, then the Indian Creek Amphibolite and the Russell Ranch Formation and their periods of intense deformation are older than Permian.

Recent work has been done on similar rocks with similar deformational histories in California, Oregon, and Idaho by Davis and Lipman (1962), Lipman (1964), Thayer and Brown (1964), Swanson (1969), and Page (1970).

A review of these works suggests, on circumstantial evidence, that the pre-Tertiary rocks in the White Pass area may be genetically related to the other Pacific Coast Paleozoic and Mesozoic eugeosynclinal rocks. The White Pass region lies along the Olympic-Wallowa lineament (Wise, 1963), suggesting a tectonic link with similar rocks to the southeast and south.

These relations make it possible to propose another history for the White Pass pre-Tertiary rocks.

The blocks of limestone and the amphibolite, in this interpretation, were brought next to the Russell Ranch Formation during large scale faulting. Except for a few large blocks, the Pennsylvanian-to-Permian limestone was in places eroded away, elsewhere buried under volcanics long after this deformation. The overlying Ohanapecosh Formation of Eocene age is only mildly deformed. Thus, the history of the pre-Tertiary rocks in the White Pass region may be bracketed between upper Paleozoic and Eocene time. In the light of the sketchy evidence presented here and the history of the eugeosyncline as outlined by Page (1970), the Russell Ranch Formation and the intense deformation are possibly Mesozoic in age (late Jurassic and Cretaceous).

Structure of the Tertiary Rocks

A geologic map of the White Pass area is given in Figure 9 and structure sections are shown in Figure 10.

Folds

The axis of the Chinook Pass anticline and the axis of the Cascade Mountain anti-



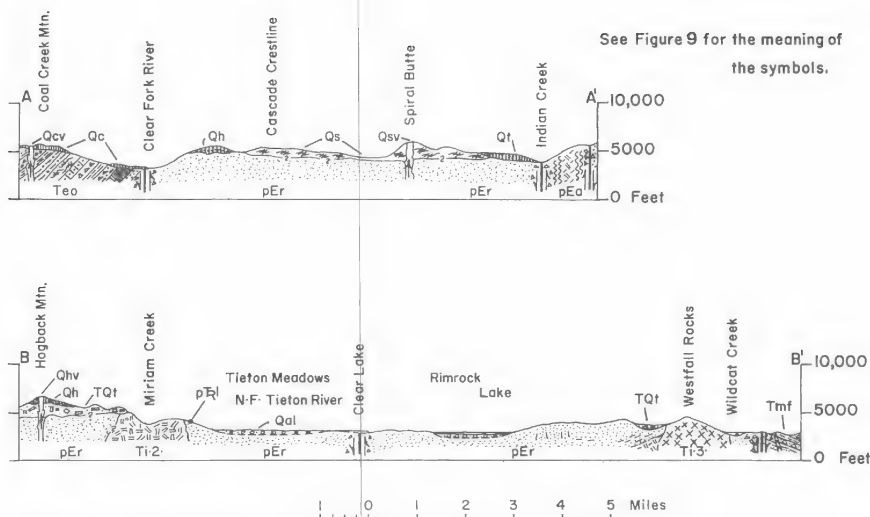


Figure 10. Structure sections of the White Pass Region.

clinorium are parallel in the White Pass area. The axial trace of the anticline is along Indian Creek, five miles east of the Cascade Crest.

The Chinook Pass anticline (Fiske, Hopson, and Waters, 1963) is a member of a family of folds trending north-northwest toward the Puget Sound lowland. These folds are part of an upper Eocene to lower Miocene mountain system that Mackin and Cary (1965) call the Calkins Range.

The axial trace of the Unicorn Peak syncline (Fiske, Hopson, and Waters, 1963) lies 12 to 14 mi west of the axial trace of the Chinook Pass anticline. The Ohanapecosh Formation dips 28° to 65° to the west along the Clear Fork River and forms the common limb of these two folds.

The Chinook Pass anticline has been locally distorted by faulting and by forceful intrusion of the Jug Lake pluton. Coal beds near the base of the Ohanapecosh Formation in Summit Creek have been overturned and dip 70° to the east. The intensity of the folding and faulting in the coal beds and the close proximity of the Jug Lake pluton have raised the grade of this coal to low-volatile bituminous or semi-anthracite (Ellingson, 1968).

East of Rimrock Lake, the Fife Peak Formation and the Yakima Basalt of Miocene age have been folded into east-west trending folds. The folding of these rocks began in early Pliocene time (Waters, 1955) and marks the beginning of the Cascade uplift. These east-west folds have changed the attitudes of the beds so that the eastern limb of the Chinook Pass anticline is poorly defined.

The uplift of the Cascade Range during the Pliocene and Pleistocene and the downwarping of the Puget Sound lowland give the Calkins folds an 8° to 10° plunge to the north-northwest in the White Pass area. The Chinook Pass-Cascade arch is breached exposing the pre-Tertiary rocks in the core of the range.

The Ohanapecosh Formation is over 10,000 ft thick west of the Clear Fork River on Coal Creek Mountain. No trace of the Ohanapecosh Formation is found four miles

to the east at White Pass. The oldest exposed rocks east of Rimrock Lake are upper Oligocene and lower Miocene ash flows and the Miocene Fifes Peak Formation (Swanson, 1966). The Fifes Peak Formation is absent from the center of the range except for two or three small outcrops of rocks that may be remnants of it.

Folding and faulting in Tertiary time have kept the White Pass region a positive area since the late Eocene. The Ohanapecosh Formation has been completely removed by erosion east of the Clear Fork fault zone at White Pass. The Fifes Peak Formation may have never been very thick in the White Pass area and no trace of it is found in the Goat Rocks Wild Area to the south.

Faults and Intrusive Activity

The Clear Fork fault zone extends to the south from Carlton Creek, across Summit and Cortright Creeks, then parallels the valley of the Clear Fork River. The fault zone continues to the south through Tieton Pass to Black Thumb and Gilbert Peak. The fault zone follows the strike of the coal beds and other incompetent beds in the base of the Ohanapecosh Formation and follows the unconformity between the Tertiary and pre-Tertiary rocks. The zone is nearly vertical indicated by its relatively straight trace across irregular topography.

The Wildcat Creek shear zone one mile east of the outlet of Rimrock Lake strikes N 45° E. Small andesite intrusions of middle(?) Miocene age were emplaced in the shear zone during faulting (Swanson, 1966). This zone has not been mapped to the north or south of the Tieton River valley.

The horst between the Clear Fork fault zone and the Wildcat Creek shear zone is approximately 18 mi wide in an east-west direction through White Pass. The main bodies of the Jug Lake pluton and the hypabyssal rocks at the eastern end of Rimrock Lake were forcefully injected into the pre-Tertiary and lower Tertiary formations along pre-existing faults or faults which formed during intrusion of the plutons. The Twin Peaks pluton lies entirely within the Russell Ranch Formation. The plutons are highly jointed but have not been faulted. The plutons tend to act as relatively immovable masses in the horst suggesting that they are cupolas of a single intrusive body underlying the horst.

Faulting during early Pleistocene time took place in White Pass on the north side of the Twin Peaks pluton and along Indian Creek. The western half of the horst, called the Tumac Plateau, was downthrown along Indian Creek tilting the plateau to the southeast. The fault in Indian Creek follows the fault zone on the west side of the Indian Creek Amphibolite.

The early Pleistocene age of the faulting is indicated by the abrupt termination of the Tieton Andesite at White Pass and the ponding of the Spiral Butte Andesite against the fault scarp. Rhyolitic ash at Bootjack Rock on Russell Ridge and outcrops of similar ash on the west side of Indian Creek indicate a possible vertical displacement of 2300 ft at the southeastern corner of the Tumac Plateau.

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Habitat Improvement—The Way to Higher Wildlife Populations in Southeast Washington

A quarter century ago southeast Washington supported abundant populations of upland birds, particularly the ring-necked pheasant. Also, there were California quail and gray partridges, commonly called Huns, in plentiful numbers. Unfortunately, these popular and beneficial birds declined drastically, notably during the last decade. Scientific studies on wildlife conducted in this region during the past 30 years provide considerable information relevant to this decline.

First, there are years of high numbers and years of low numbers. These year-to-year fluctuations are unpredictable and not subject to control by the farmer or the wildlife manager since they are primarily caused by weather conditions during the reproductive season in spring. Studies by Buss and Swanson (1950) revealed the importance of weather during the reproductive season. Their studies compared hatching dates for 1948, an exceptionally wet year, and 1949, a relatively dry year, for the ring-necked pheasant in the Palouse area. Seventy-one hatching dates for 1948 showed that most nests hatched from June 15 to 28, whereas 117 hatching dates for 1949 showed that most nests hatched between May 28 and June 4, over two weeks earlier than the hatching peak of 1948. The delay in hatching during the wetter year of 1948 increased mortality of nesting hens by prolonging the breeding period and attendant reproductive stress. Also, the wetter conditions contributed to greater mortality in broods. Thus, when weather conditions are favorable for reproduction, fall populations are relatively high, reflecting what is called a "good" year. Conversely, unfavorable weather conditions result in a "bad" year. These annual fluctuations are important since they can be dramatic in extent, characteristic for all of southeast Washington, and as indicated above, they are not within our control. These fluctuations are mentioned, however, only to point out their presence and cause. The long-term population trend is of primary concern, not the short-term.

When the irregular population numbers of upland game birds for southeast Washington for the last 30 years are studied, a definite downward trend in average numbers is noted. This long-term downward trend reflects a deteriorating environment, specifically dwindling habitat conditions throughout southeast Washington. The major habitat component which has deteriorated is cover. Causes of both the long- and short-term trend emerge from several studies conducted in southeast Washington.

A study by Buss and Dziedzic (1955) showed how dramatic the correlation between habitat reduction and a specific wild population can be. This case concerns

a shrub and grassland species, the sharp-tailed grouse, and the effect of man's activities, primarily agriculture, on the habitat which originally supported this abundant game bird. Cultivation began in the mid-1870's and was increasing rapidly by the 1890's. At this time a decline in the population of sharp-tailed grouse was noticeable, although it was not yet of great importance. About 1910, however, the amount of available cover had reached and in fact passed a critical point as far as the survival of the sharp-tailed grouse was concerned. In a single decade from 1910 to 1920 the population plummeted below the threshold of survival. This drastic reduction was accompanied by restrictions on hunting limits and reductions in seasons until in 1919 the season was closed in Whitman County; it has never opened again. These actions were all to no avail. The increasing demand of agriculture resulted in more land being placed under the plow, until the situation became intolerable for the dwindling remnants of sharptails. By the late 1940's their extirpation from the Palouse region was complete.

A long-range study involving population trends of upland game birds was conducted on a study area called the Colton Plot. This plot is typical of agricultural land in southeast Washington and has been studied intensively by various investigators for the past 30 years. The area is 2560 acres in size, located seven mi south of Pullman and four mi northwest of Colton along Union Flat Creek, and ranges from 2450 to 2800 ft in elevation. Figure 1 compares plant cover on the Colton Plot in 1940 (Swanson and Yocum, 1958) with cover remaining in 1966. The hatched areas show the natural habitat which existed on the area as of 1940, when studies of the Colton Plot began, and the greatly reduced habitat remaining in 1966. This process of habitat reduction has not been a precipitous one but one of gradual whittling away at remaining areas of cover. In addition, there has been a reduction of acreage in alfalfa (76 percent from 1940 to 1958) and the amount of stubble left over winter. Stubble-field plowing is of great importance as these fields, once plowed, are of little value as food or cover for game birds. Field work has indicated that brushy draws bordered by standing stubble are important wintering areas. In areas like the Colton Plot with highly productive agricultural lands, there is continual effort to increase crop production, especially by progressively cultivating a higher percentage of the land. As more and more land is cultivated, less favorable areas are put into production. Steeper slopes are plowed, stream banks are cleared, gullies are debrushed, and woodlots fall to the axe. Consequently, wildlife cover is so drastically reduced that it becomes the principal limiting factor in maintenance of all wildlife populations. In the past there was evidence of this problem in the "eyebrows" of grassy patches left unplowed on steep slopes, in fence-row thickets, and in cul-de-sac gullies of *Crataegus* and other shrubs. More recently the increase in size of farms, the reduction of fence-rows (particularly line fences), and the elimination of stream-bank vegetation with bulldozers has resulted in elimination of even token cover areas. Clearly, today's critical shortage of cover requires more than chance patches of food and cover left in the wake of bulldozer and gang plow. The time is here for major changes in patterns of land use; changes beneficial not only to wildlife but also to flood control and soil conservation.

Swanson and Yocum (1958) studied the populations of pheasants and gray partridges on the Colton Plot in relation to habitat. Figure 2 is based in part on their report and shows that the overall trend is to a lower and lower pheasant population.

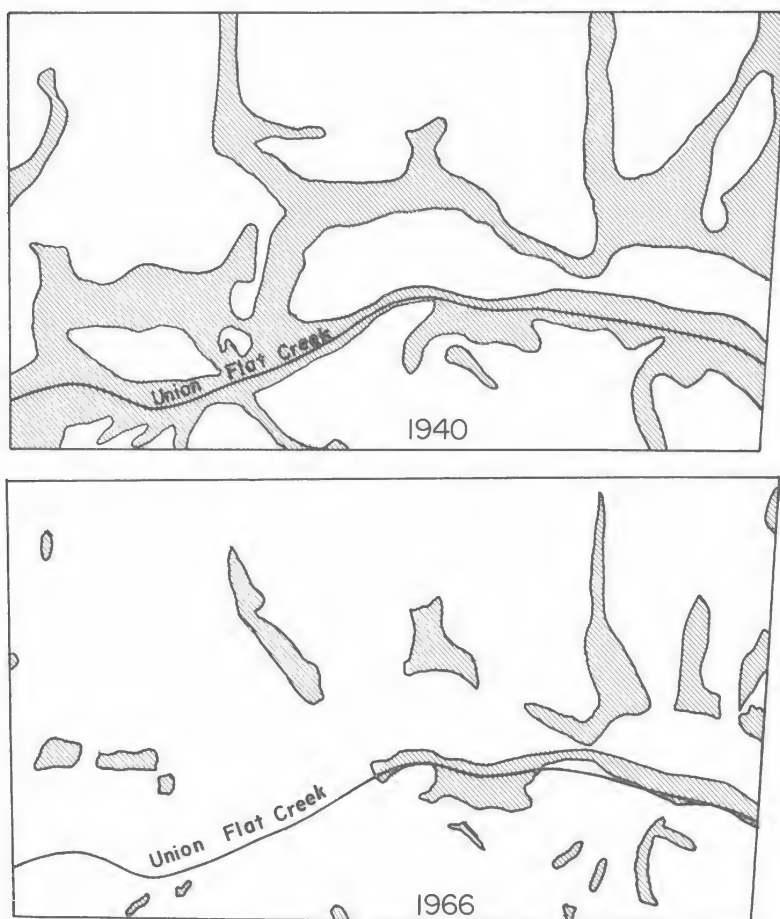


Figure 1. Representative section of Colton Plot, four miles northwest of Colton, Whitman County, Washington. Cross-hatched areas show reduction in permanent cover between 1940 and 1966. Scale: 1" = 410 feet.

There are year-to-year fluctuations in fall pheasant numbers but these, as stated above, are generally a reflection of weather conditions during the preceding breeding season. Figure 2 also shows the population trend of gray partridges during this same period. Clearly, the year-to-year fluctuations and the long-term decline of both partridges and pheasants closely follow the continually diminishing trend in habitat. Swanson and Yocum (1950) concluded that these population curves indicate: (1) breeding populations are governed by habitat, and (2) fall populations indicate the type of weather during the reproductive season. The long downward trend of declining game-bird populations, basically the breeding population, must be recognized and reversed. No single individual, no single bureaucratic agency, no single governmental unit is going to be able to do this alone. The causative factors of environmental deterioration must

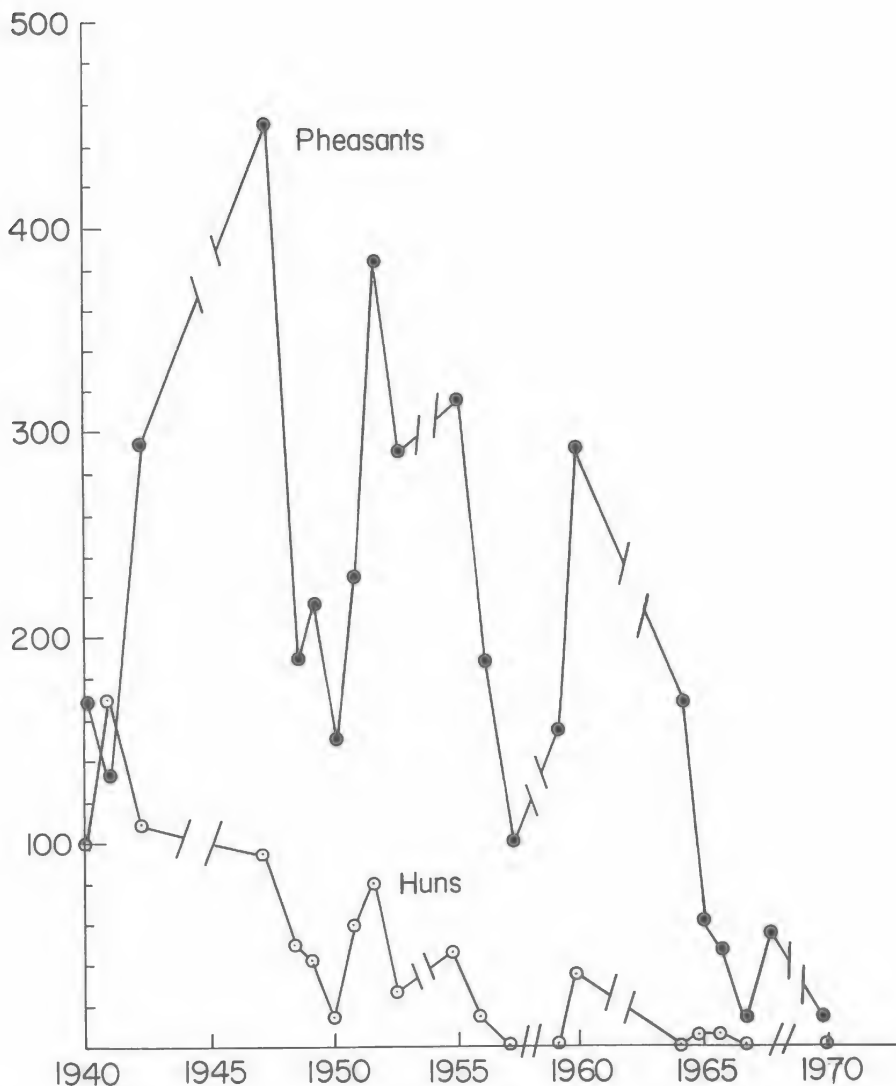


Figure 2. Downward trend in pheasant and Hungarian partridge populations on the Colton Plot, Whitman County, Washington, 1940-1970.

be recognized by every concerned person and agency and coordinated action taken to correct the situation.

The two following approaches to the problem of a declining wildlife population are not new. Artificial propagation or stocking and environmental improvement have been studied and used frequently in attempting to bolster populations of desirable wildlife species. In almost every case habitat was shown to be the limiting factor

and without habitat improvement, repopulation simply will not occur. Rarely is a high-quality wildlife habitat found uninhabited, and in these rare cases stocking does result in re-establishment of a wild population.

Steen (1950) reported on a study for which the restorative results of three years of bobwhite quail stocking, followed by three years of environmental improvement, were measured and compared. The entire experiment was conducted on the same study area, with a comparable tract being used as a check area. On the study area the fall population continued to decrease during the first three-year period even with the stocking of approximately 120 birds prior to the breeding season each spring. Habitat improvement on the study area included pasture improvement, pond construction, and fence-row, waste area, and wildlife border improvement. Carrying capacity of the improved area was raised from one bird per 10.7 acres in 1945 to one bird per 3.4 acres in the fall of 1949. The total fall population rose from 252 quail before land management began to 605 birds by the fall of 1949. This study showed that: (1) habitat improvement is effective in re-establishing wild populations, (2) habitat improvement can be attained through recommended land-use practices, and (3) the route to increased wild populations is through better land use.

Significantly, continuous intensive hunting pressure was present on the area throughout the period. Fall populations were shot down to what was thought to be dangerously low levels yet sufficient breeding stock remained to produce increased populations each year. Additionally, this was a cooperative program involving farmers and landowners, Agricultural Extension Service, Soil Conservation Service, and the local Wildlife Research unit. Standard benefits for approved practices were paid by the Production and Marketing Administration and matched by Olin Industries to all participating farmers. The farmers did not suffer economically and wildlife populations were restored.

If declining wild populations are to be restored in southeast Washington, it will be accomplished through habitat improvement, not stocking. What can be done to improve habitat; how does one go about it; and, most importantly, who is going to take the initiative to get the program started? Following are some suggested answers to these questions.

Farming methods in southeast Washington have resulted in large amounts of rill and sheet erosion, as much of the rainfall in the region comes when crop cover is at its lowest. Over 97 percent of the land in Whitman County is under cultivation. To provide adequate cover for wildlife and reduce serious erosion problems, some land must be returned to uses which do not require annual plowing and fallowing. Most of the soil removed by erosion is carried far downstream and lost permanently from the watershed. This is in itself a process that cannot go on forever and must be considered when planning improvement for wildlife populations.

The permanent re-establishment and preservation of natural riparian vegetation along all stream banks and the revegetation of marginal lands in cul-de-sac gullies and on steep slopes should be adopted. The benefits of such a program both to wildlife and the environment generally would be enormous and would accrue to the farmer as well as to the general public. First, a permanent, continuing source of cover and food would be provided, especially for upland game birds, semi-aquatic fur bearers, and small riparian species. The perennial vegetation provided would stabilize the soil and prevent its erosion into the stream. Also, stream banks would be stabilized

reducing channel erosion. Presence of vegetation would act as a filter for surface runoff from surrounding cultivated fields, further reducing the amount of sediment reaching streams. Stabilizing stream banks would increase channel depth and lower water temperatures, providing habitat for preferred species of game fish. Additionally, the presence of vegetation would provide shade for the stream, also keeping the temperature down and further favoring the existence of game fish. Finally, vegetation would increase the moisture-holding capacity of soil thus slowing rapid runoff into the stream such as now occurs in times of rapid thaw coupled with heavy rainfall. Thus, flooding would be reduced or in some cases prevented.

Keeping soil from eroding into streams would reduce turbidity, improving conditions for game fish and eliminating or reducing the amounts of fertilizers and pesticides which flow in with soil particles keeping water quality at acceptable levels from a biological viewpoint. Excessive amounts of fertilizer in the water often increase stream fertility favoring growth of algae and subsequently lowering the oxygen content below that required for the survival of game fish.

How could this type of program be instituted in a manner that would be feasible and fair to the landowner? Specifically, a strip of native riparian vegetation should be established along both sides of all streams. This strip should average 25 ft in width, and not necessarily or desirably follow a stream exactly as the stream flows but rather should tend to straighten it some. Thus, where a bend occurs this strip should be wider than 25 ft on the inside and narrower than 25 ft on the outside of the bend. This would benefit wildlife by providing some relatively large areas of cover and benefit the farmer by giving him a relatively straight field border to work, rather than following the winding course of the stream. All marginal areas and steep slopes which have been cultivated would be replanted with native vegetation and retained permanently to provide scattered cover throughout the region.

The farmer could be compensated for the loss of this land to production by federal or state lease and then paying him to manage the land according to established management principles. This would of course also represent acreage taken out of wheat production as far as the wheat withdrawal program is concerned. Supporting government programs for habitat improvements are discussed by Moorman and Kowalski (1966) in connection with improved hunting for pheasants and quail.

Nearly everyone is familiar with the wheat withdrawal program that provides subsidies for land withheld from production. Farmers do what is necessary to obtain maximum productivity, that is to say, maximum dollar return, from their lands. Considering the farmer's economy, the need for increasing cover, and the importance of reducing erosion, one possibility exists that might accomplish all three. Specifically, return some of the cultivated land on steep slopes to grassland for grazing or production of hay crops. This would diversify the farmer, putting him into hay or beef production or both, stabilize those areas which are converted to grassland, and increase the amount of available cover. If this proved uneconomical then perhaps an extension of the wheat withdrawal program or a new program based on the same principles could be instituted to subsidize the farmer for any loss incurred by removing parts of his acreage from wheat production. The cost of this program could be offset in part by reduction in the cost of artificial restocking of pheasants and other game animals and reduction in flood control and soil conservation programs. The intrinsic values of increased natural populations would be important and would not be restricted

to upland game birds but many other less well known but important species. The actual mechanics of selecting what lands would be withdrawn, what specific use they would be turned to, and how long they should be withdrawn could be determined by investigation of the variables themselves. A possibility which could further enhance the value of the program would be to withdraw lands for certain periods of time, say eight years, and then return these lands to grain production and replace them by withdrawing new lands. This would have the effect of returning much needed natural nutrients to the soil every few years, particularly in those areas where legumes were produced on withdrawn lands. This possibility is worthy of serious consideration.

These two suggested plans are not panaceas for curing all the environmental ills of the land in southeast Washington. They are useful means, however, to improve significantly the environment of this area. Either one would dramatically improve wildlife; both together would yield by far the greatest improvement in all environmental respects. These programs would not be difficult to administer, would cost the taxpayer no additional money in the long run, and would benefit the farmer economically.

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Rhodophylloid Fungi of the Pacific Coast (United States) II: New or Interesting Subgeneric Taxa of *Nolanea*

The rhodophylloid fungi (sensu Largent and Benedict, 1971) belong to the Agaricales and are distinguished most readily by their pink, angular basidiospores. Although these mushrooms constitute a major element in the agaric flora of the Pacific Coast, little is known about their ecology, distribution, or taxonomy in this region. Most early reports in the literature are either lists of different species collected or contain such inadequate descriptions that their identification could easily be challenged.

One of the earliest reports was that by Harkness and Moore (1880) who published a catalogue of agarics of California which included eight species of rhodophylloid fungi. In papers on Oregon fungi both Zeller (1933) and Kauffman (1925, 1929) published lists, descriptions, and new species. Included in these series were *Claudopus affinis* Kauff., *C. byssisedus* (Pers. ex Fr.) Gillet, *C. nidulans* (Pers. ex Fr.) Karsten, *C. subargillaceus* Kauff., *C. variabilis* (Pers.) Gillet, *Eccilia bispora* Kauff., *Entoloma nidosum* (Fr.) Quél., *E. nitidum* Quél., *E. speculum* (Fr.) Quél., *Leptonia asprella* (Fr.) Quél., *L. formosa* (Fr.) Gillet, *L. fusciceps* Kauff., *L. placida* (Fr.) Kummer, *L. serrulata* (Pers. ex Fr.) Kummer, *L. subeuchroa* Kauff., *L. trivialis* Kauff., *Leptoniella fuliginosa* Murr., *L. occidentalis* Murr., *Nolanea mammosa* (L. ex Fr.) Quél., and *N. pascua* (Pers. ex Fr.) Kummer.

Nine species were reported from Washington by Murrill (1917) and Kauffman (1925). These were *Claudopus commixtus* Kauff., *C. cortincinctus* Kauff., *C. nidulans* (Pers. ex Fr.), *Entoloma sericiceps* Murr., *E. washingtonense* Murr., *Leptonia fusciceps* Kauff., *Nolanea latifolia* Kauff., *N. mammosa* (L. ex Fr.) Quél., and *N. occidentalis* Murr.

Finally, Earle (1905), Murrill (1917), and Peck (1895) published studies on west coast fleshy fungi and reported the following species of rhodophylloid fungi: *Claudopus avellaneus* Murr., *C. nidulans* (Pers. ex Fr.) Karst., *Eccilia californica* Murr., *E. nigricans* Peck, *E. yatesii* Murr., *Entoloma ferruginans* Peck, *E. plumbeum* (Earle) Murr., *E. sericiceps* Murr., *Leptoniella edulis* (Peck) Murr., *L. fuliginosa* Murr., *L. nigra* Murr., *L. occidentalis* Murr., *Nolanea mammosa* (L. ex Fr.) Quél., and *N. pascua* (Pers. ex Fr.) Kummer.

Of those rhodophylloid fungi reported from the West Coast, *Claudopus nidulans* has smooth spores and has been transferred to *Phyllotopsis* (Singer, 1936); *Entoloma plumbeum* Earle has smooth spores and may be a species of *Lepista* (Hesler, 1963). Similarly, *Claudopus affinis* Kauff., *C. cortincinctus* Kauff., *C. subargillaceus* Kauff., and *Eccilia bisporea* Kauff. have smooth spores and should be excluded from further study as rhodophylloid fungi (Largent, 1971).

In addition to the published reports mentioned above, several mycologists have collected these fungi on the Pacific Coast but no published results of their work have been found. Because local amateurs frequently sent collections to Peck, Atkinson, Murrill, and others for identification, numerous collections were deposited in such herbaria as that of Harvard University, New York Botanical Garden, New York State Museum at Albany, and Cornell University.

Macrochemical spot tests: "Two or three drops of chemical reagent (Table 1) were added to small triangular pieces of fresh carpophore, including pileus, lamellae, and apex of stipe (if possible), in a spot plate. After 10-12 minutes, color changes were observed and recorded." (Largent and Benedict, 1971)

TABLE 1. Macrochemical spot test reagents.

alpha-Naphthol:	10 gm in 70 ml 95% ethanol; bring total volume to 200 ml with water.
Aniline-Water:	50% v/v with water.
Chloral Hydrate:	conc. aq. soln.
Guaiac:	Supersaturated soln. of finely ground gum guaiacum in 95% ethanol; filter.
Guaiacol:	saturated aq. soln.
Ferric Sulfate:	10% aq. soln.
p-Dimethylaminobenzaldehyde (PDAB):	2% in 76 ml ethanol and 24 ml conc. HCl.
Phenol:	2% aq. soln.
Phenol-Aniline:	3.0 drops oil of aniline and 5.0 drops conc. (reagent) sulphuric acid in 10.0 ml 2% phenol.
Pyrogallol:	10% aq. soln.
Selenium Dioxide:	2% aq. soln.
Sulphuric Acid:	50% v/v with water.

Microchemical techniques: The following techniques were used to aid in the study of microscopic characters:

1. *Carminophilous Granulation:* see Grund and Marr, 1965.
2. *Techniques to study granules in the hyphae:* see Kühner and Romagnesi, 1953.
3. *Metachromatism:* see Kühner and Romagnesi, 1953.
4. *Techniques to study the topography of pigments:* (paraphrase from Kühner and Romagnesi, 1953). Prepare a solution of Picroformol of Holland as follows: Crush 2.5 mg neutral copper acetate into a fine powder with a mortar and pestle and dissolve in 1000 cc water; add 4.0 gm picric acid, little by little, while constantly stirring. After the picric acid has dissolved, add 10.0 cc Commercial Formalin and 1.5 cc Glacial Acetic Acid. *For Dried Specimens:* Immerse the tangential sections of lamellae and radial sections of the pileus in the Picroformol of Holland solution for at least five minutes. Remove the sections, place them in three drops of freshly prepared concentrated chloral hydrate in a watch glass. Place the watch glass over a low flame and bring to a boil. Observe immediately in concentrated chloral hydrate. *For Fresh Specimens:* Immerse radial and tangential sections in a drop of concentrated sugar or salt solution on a microscope slide. Observe immediately.

Abbreviations used in the taxonomic descriptions:—Abbreviations used to describe these fungi are as follows: P.T. = pileal trama, P.S. = pileal surface, L.S. = lamellar surface, S.T. = stipe trama, S.S. = stipe surface, L = length, D = diameter, L-D = length minus the diameter, and L/D = length divided by the diameter.

Measurements were made of ten different spores, basidia, or cystidia and did not include the apiculus of the basidiospores nor the sterigmata of the basidia. The range of the length minus the diameter (L-D) measurements is given from the smallest to the largest of the ten measurements. In all cases averages were obtained by dividing the total length or width of all measurements by ten. The colors enclosed in quotation marks are those of Ridgway (1912). All others are from Kornerup and Wanscher (1961). For example, (6, A, 2-3) indicates the page, row, and column, respectively.

The collections are deposited either in the cryptogamic herbaria of San Francisco State College (SFSC) or of Humboldt State College (HSC).

Nolanea (Fr.) Kummer emend. Largent & Benedict, Madrono 21: 36. 1971.

Species of *Nolanea* can be characterized by the following combination of features: "clamps absent or rare; pileal surface glabrous, dry or lubricous; pileal cuticle of repent hyphae; urea concentration high" (Largent and Benedict, 1971, p. 38-39). *Nolanea* species can be distinguished from some species of *Entoloma* by the pileal cuticle whose hyphae are well differentiated from those of the pileal trama, by the absence or rarity of clamp connections, the less fleshy carpophore, and more reliably by the high urea concentration. *Leptonia*, *Pozzaromyces*, and *Alboleptonia* all differ from *Nolanea* by virtue of the different structure of their pileal cuticle, and their low urea content.

1. *Nolanea* (Fr.) Kummer em. Largent & Benedict, Section *Holoconiotae* sect. nov. Superficies stipitis pruinosa apice. Hyphae cuticulae non incrustatae. Sporae ovata vel elongato-angulatae. Caulocystidia abunda, solitaria, cylindrica.

Typus: *Nolanea holoconiota* Largent & Thiers

Surface of the stipe pruinose for at least the apical half. Hyphae of the pileal cuticle without any external incrustations. Spores ovate- to elongate-angular, not stellate-angular nor prismatic. Caulocystidia abundant, solitary, long, cylindric, and originating from the middle of the surface hyphae of the stipe. Clamp connections absent on the cuticular hyphae of the pileus, present or absent at the bases of the basidia and basidioles or at the crosswalls of the hyphae of the basal tomentum.

Type species: *Nolanea holoconiota* Largent & Thiers.

a. *Nolanea holoconiota* sp. nov.

Pileus 10-80 mm latus, conicus vel convexus vel planus, glaber vel appresso-fibrillosus, sub-brunneus vel fulvus demum pallido-aurantiacus vel griseo-luteus. Lamellae annexae vel ascendenti-adnatae, confertae vel subdistantae, albae vel pallidae demum subroseae. Stipes 35-100 mm longus, 3-7 mm latus, apice pruinosis, glaber vel appressus subter, luteus vel sub-aurantiacus. Sporae 9-13 x 6.5-9 μ , elongato-angulate. Cheilocystidia rostrato-ventricosa, 50-100 x 8-15 μ . Pleurocystidia absentia.

Typum legit D. L. Largent, n. 274, Payette Lakes, Payette Nat'l Forest, June 16, 1962. In herbario Humboldt State College conservatum.

Pileus. 10-80 mm broad, 10 mm high, conic to convex becoming subconic to broadly conic or even plane, apiculate to acutely umbonate at all times; surface glabrous to silky appressed-fibrillose, rarely obscurely fibrillose-scaly on the margin, dry, hygrophanous, appearing atomate or micaceous on fading, at times obscurely wrinkled or corrugate; light brown or yellowish-brown (5-6, C-D, 4-6; "Olive Brown," "Buffy Brown," "Deep Olive Buff," or "Saccardo's Umber") at first, becoming pale orange to grayish orange to grayish yellow (4-5, A-B, 2-3; "Olive Buff," "Warm Buff," "Light Buff," "Cream Buff," "Colonial Buff," to near "Chamois" or "Honey Yellow"), apiculus often brighter than the remaining portion; margin incurved to decurved, at times flared, typically eroded and rimose with age, translucent-striate when moist; context 1-3 mm thick, almost white to "Pale Olive Buff," unchanging; taste unpleasant to slightly bitter, at times not distinctive; odor not distinctive. *Lamellae*: narrowly adnexed or ascending adnate, close to subdistant, at times distant, 3-5 mm broad, 9-15 mm long, white to pallid ("Deep Olive Buff") becoming pinkish ("Vineaceous Buff," "Tilleul Buff," "Pinkish Buff," "Light Pinkish Cinnamon," "Wood Brown," to "Drab"); margin entire, concolorous. *Stipe*: 35-100 mm long, 3-7 (-15) mm broad at the apex; equal or tapering in either direction; terete to occasionally compressed and grooved; surface pruinose on the upper two-thirds to one-half, at times completely so, otherwise glabrous to appressed-fibrillose, longitudinally-striate; pale yellow to light yellow or pale orange to light orange (4-5, A-B, 2-3, "Pale Olive Buff," "Deep Olive Buff," "Olive Buff," "Warm Buff," "Pale Ochraceous Buff"); context stuffed then hollow, concolorous with the pileal context, unchanging when bruised; basal tomentum white and abundant.

Spores 9-13 x 6.5-9 μ , average length 10.9 μ , average width 7.8 μ , L/D 2.5-5.5 μ (average 3.1 μ), elongate-angular, 5-6 sided, asymmetrical. Basidia 30-43 x 11-14 μ , average length 36.9 μ , average width 12 μ , average L/D 3.0, clavate, four-spored. Cheilocystidia rostrate-ventricose, somewhat capitate at times, colorless, infrequent to abundant, more obvious near the pileal margin, 50-100 x 8-15 x 4-7 (apex) μ , average length 69.7 μ , average width 10.8 μ , average L/D 6.4. Pleurocystidia absent. Hyphae of the lamellar trama up to 35 μ wide. Pileal cuticle a loosely entangled trichodermium, often obscure, becoming repent away from the disc; terminal cells cylindric to slightly clavate, colorless, 35-140 x 4-6 μ , average length 83.8 μ , average width 5.0 μ , average L/D 16.8. Cuticle at the apex of the stipe a loosely entangled trichodermium; caulocystidia cylindric, rarely rostrate-ventricose, most often originating from the middle of the surface hyphae, solitary and abundant, 45-125 x 7-15 x 5-7 μ , average length 86.1 μ , average width 11.1 μ , average L/D 7.8. Stipe trama of more or less parallel phayae (up to 35 μ wide). Lactifers rare to abundant in the pileal trama. Incrustations absent on all hyphae. Clamp connections absent.

Macrochemical Reactions: Pyrogallol—positive in all parts of the basidiocarp. Guaiac, Guaiacol, alpha-naphthol, PDAB, and Selenium Dioxide negative. Other reagents not studied.

Habit and Habitat: Solitary to scattered in mossy humus or needle humus beneath Douglas Fir, Mountain Hemlock, various Pines, or Western Red Cedar. Often at or above 3000 ft.

TYPE: IDAHO: Valley Co.: Scattered to gregarious in humus of dense mixed coniferous forest, 16 June 1962, *Largent* 274 (HOLOTYPE: HSC), Payette Lake, Payette National Forest.

Additional Material Studied: CALIFORNIA: Alpine Co.: *Thiers* 16575, 16740, 16864; Amador Co.: *Breckon* 418, 443, 459, 460, *Sundberg* 484, 485, *Thiers* 20008, 20026, 20038, 20073, 20077, 20086; Calaveras Co.: *Thiers* 16750, 16797; Fresno Co.: *Thiers* 19459; Mariposa Co.: *Thiers* 19709; Shasta Co.: *Thiers* 12716, 12766, 12832, 12884; Sierra Co.: *Thiers* 12588, 19517; Siskiyou Co.: *Thiers* 19577; Tuolumne Co.: *Thiers* 12652, 19492, 19815, 21012, 21018. IDAHO: Adams Co.: *Largent* 297, 321, 392; Custer Co.: *Largent* 547, 586; Valley Co.: *Largent* 289, 290, 314, 350, 403, 404, 416, 417, 454, 664. WASHINGTON: Island Co.: *Largent* 2627 2654, 2726; King Co.: *Largent* 1680, 1708, 1863; Pierce Co.: *Largent* 1364; San Juan Co.: *Largent* 2554; Snohomish Co.: *Largent* 1392, 1766.

Nolanea holoconiota can be recognized by its conic and apiculate, light brown to yellowish brown pileus, pale yellow to pale orange stipe that is pruinose on the apical one-half to two-thirds portion, the rostrate-ventricose cheilocystidia and the cylindric caulocystidia that often originate from the middle of the surface hyphae.

Several rhodophyllid fungi that resemble *Nolanea holoconiota* in one or more points are listed below.

(1) *Entoloma luteum* Peck has four-sided spores, "Primuline yellow" lamellae, clavate cheilocystidia and clavate-cylindric caulocystidia that are similar to the pileocystidia.

(2) *Nolanea myceniformis* Peck has cylindric cheilocystidia (28-33 x 5.5-7 μ), no odor, an "avellaneous" pileus with a darker disc, and a cartilaginous stipe (40 mm long, 1-2 mm broad at the apex).

(3) *Entoloma pallidipes* Hesler has a "Pale Pinkish Buff" pileus, a cartilaginous stipe (30-50 mm long and 1-1.5 mm broad at the apex), and no caulocystidia.

(4) *Nolanea conica* Peck has smaller spores (8-11 x 6-7.5 (-8) μ), cylindric-clavate caulocystidia that do not originate from the middle of the hyphae and no cheilocystidia.

The photograph of *Entoloma strictius* var. *cystidiosum* Hesler (Hesler, 1967) appears similar to *Nolanea holoconiota*. However, *E. strictius* var. *cystidiosum* differs by having a "Snuff Brown" pileus when moist, a white to pallid to dingy brownish stipe, and no caulocystidia.

We feel the distinct caulocystidia and the nature of the stipe surface are sufficient to warrant proposing a new section, *Holoconiota*, for *Nolanea* with *Nolanea holoconiota* as the type species.

2. *Nolanea* (Fr.) Kummer em Largent & Benedict, Section *Cosmeoexonema* sect. nov.

Sporae elongatae vel ovatae, angulatae, pentagonae vel hexagonae. Hyphae cuticulae incrustatae.

Typus: *Nolanea sericea* (Bull. ex Mérat) Orton.

Spores elongate- or ovate-angular (4-) 5-6 sided, not stellate-angular nor prismatic. Hyphae of the pileal trama or pileal cuticle with external incrustations.

Type species: *Nolanea sericea* (Bull. ex Mérat) Orton.

a. *Nolanea bicoloripes* sp. nov.

Pileus 10-35 mm latus, umbonatus vel apiculatus vel papillatus, e fibrilloso glaber, subaurantiacus demum brunneus vel fulvus. Lamellae annexae vel adnatae, confertae vel subdistantes, albae demum subroseae. Stipes 35-95 mm longus, 0.5-3.5 mm latus, subtiliter squamulosus apice, glaber subter, subaurantiacus demum brunneus. Sporae 7-8 x 5.5-7 μ , ovate, angulatae. Cystidia absentia.

Typum legit D. L. Largent, n. 1574, Snohomish Co., Washington, Sept. 14, 1966; in herbario Humboldt State College conservatum.

Pileus: 10-35 (-40) mm broad, 5-20 mm high, versiform in shape, acutely umbonate or apiculate or papillate, the umbo often lost with age; at first covered by abundant superficial fibrils, often glabrous with age, fades readily, at times zonate; at first pale orange or orange-white to orange-gray or grayish orange (5-6, A-B, 2-4), then darkening to light-brown to dark yellowish brown (5-6, D-E, 2-5), the umbo often lighter; margin incurved then decurved,

entire becoming eroded, smooth, not translucent; context up to 3 mm thick near umbo, whitish to buff-white; taste and odor not distinctive or, at times, slightly unpleasant. *Lamellae*: adnexed to narrowly adnate, close to subdistant, rarely distant, 2-6 mm wide, 5-22 mm long, white then pinkish; margin smooth, concolorous. *Stipe*: 35-95 mm long, 0.5-3.5 mm broad at the apex, equal and terete; at times flocculose to minutely squamulose at the apex, then glabrous; at first nearly concolorous with the lighter areas of the pileus (pale orange to grayish orange, 5-6, A-B, 2-4), then darkening from the base upward with age or with handling to light brown, yellow brown, or dark yellow brown (5-6, D-F, 3-5); context hollow, concolorous with the pileal context, unchanging.

Spores 7-8 x 5.5-7 μ , average length 7.4 μ , average width 6 μ , L/D 0.0-2 μ (average 1.4 μ), 4-5-6 sided, ovate-angular. Basidia 29-34 x 7-9 μ , average length 31.1 μ , average width 8.1 μ , L/D 3.2-4.2 (average 3.8), 4-spored, clavate. Cheilocystidia and pleurocystidia absent. Hyphae of the lamellar trama up to 20 μ wide. Cuticle on the pileal disc an entangled, interwoven trichodermium; terminal cells clavate to cylindro-clavate, colorless, 42.5-80 x 5-12.5 μ , average length 58 μ average width 7 μ , L/D 5.2-10.6 (average 8.3); hyphae of the pileal trama up to 13 μ , broad, with slight to distinct external ring-like incrustations. Apex of the stipe with scattered to abundant clusters of clavate, cylindro-clavate, colorless caulocystidia 27.5-55 x 5-13 μ , average length 37.5 μ , average width 10.3 μ , L/D 2.6-7 (average 3.6); hyphae of the stipe trama up to 20 μ broad, with distinct, abundant, external ring-like incrustations. Lactifers absent. Clamp connections absent on the hyphae of the pileal cuticle and of the stipe apex, rare at the bases of the basidia and basidioles, and scattered to rare on the hyphae of the basal tomentum.

Macrochemical Reactions.

	P.T.	P.S.	L.S.	S.S.	S.T.
Guaiac	$\pm$	$\pm$	$\pm$	—	—
Guaiacol	$\pm$	$\pm$	$\pm$	—	—
Pyragallol	+	+	+	+	+
Alpha-Naphthol	+	+	+	+	+
Selenium Dioxide	—	—	$\pm$	—	—
PDAB	$\pm$	$\pm$	$\pm$	$\pm$	$\pm$

Chloral hydrate, sulphuric acid (50 per cent), ferric sulphate, phenol aniline, aniline-phenol were all negative.

Habit and Habitat: Scattered to gregarious, rarely solitary among mosses, beneath Devil's Club, Skunk Cabbage and ferns, near Mountain Hemlock, Grand Fir, Western Red Cedar or Red Alder, in either coniferous or mixed conifer-hardwood forests.

TYPE: WASHINGTON: Snohomish Co.: Scattered in mossy humus beneath various Ferns and Devil's Club, near Western Red Cedar; Sloan Creek Campground, Mt. Baker National Forest, 14 Sept 1966, *Largent* 1574 (HOLOTYPE: HSC).

Additional Material Studied: WASHINGTON: King Co.: *Largent* 1308, 1309, 1723; Pierce Co.: 1181, 1189, 1281, 2193, 1380, 1403, 1596, 1662, 1769, 1846, 1869, 2225, 2805, 2884, 3211, 3216, 3231.

The distinctive characters of *Nolanea bicoloripes* include its versiform and papillate pileus that is covered by superficial fibrils at first, long and slender stipe that is light colored at first, and darkens from the base upward with age, white lamellae, subglobose spores, entangled trichodermium, externally incrustated hyphae, and clustered, colorless caulocystidia.

Several rhodophyllid fungi that resemble *Nolanea bicoloripes* in one or more points are listed below:

(1) *Nolanea conica* (Peck) Sacc. has clamp connections on the hyphae of the pileal cuticle, a dull watery cinnamon pileus, and larger spores.

(2) *Entoloma papillatum* (Bres.) Hesler has brown or grayish pileus, farinaceous taste, spores that are 9.5-11 μ long, and translucent-striate margin.

(3) *Entoloma prismosporum* Hesler has prismatic spores, a dingy brown pileus and a translucent-striate pileal margin.

(4) *Entoloma subumbonatum* Hesler has a grayish brown, appressed-silky pileus that is slightly umbonate at the depressed center, and lacks caulocystidia.

(5) *Entoloma subquadratum* Hesler has subquadrate to more or less cruciform spores, "Hair Brown" to "Drab" to "Olive Brown" stipe.

(6) *Entoloma mammosum* (Fr., Hesler has a rancid taste or, at times, farinaceous, has cheilocystidia and a darker colored pileus.

3. *Nolanea* (Fr.) Kummer em *Largent* and Benedict, Sect. *Endochromonema*, sect. nov.

Spores elongatae vel ovato-angulatae tetragonae, pentagonae vel hexagonae. Hyphae tramatis pileo non incrustatae.

Typus: *Nolanea cetrata* (Fr. ex Fr.) Kummer.

Spores elongate- or ovate-angular, (4) 5-6 sided, not stellate-angular or prismatic. Hyphae of the pileal trama or pileal cuticle without external incrustations.

Type species: *Nolanea cetrata* (Fr. ex Fr.) Kummer.

a. *Nolanea fructufragrans* sp. nov.

Pileus 10-20 cm latus, convexus vel umbonatus, glaber, siccus, hygrophanus, griseolo-brunneus denum subaurantiacus vel aurantiacogriseus. Lamellae adnexae vel fere liberae, confertae vel subdistantes, e sub-brunneis erubescensibus. Stipes 50-60 mm longus, 1.5-2 mm latus, apice pruinosis vel floccosis, aliter glaber, brunneus vel aurantiacus. Sporae 8-10 x 7-8.5 μ , ovato-angulatae, tetragonae vel hexagonae. Cheilocystidia et pleurocystidia absentia.

Typum legit D. L. Largent, n. 3358, Island Co., Washington, Type, Nov. 2, 1967; in herbario Humboldt State College conservatum.

Pileus: 10-20 mm broad, convex and acutely umbonate; surface glabrous, dry, hygrophanous; dark grayish brown to grayish brown (5-6, D-F, 3-5) at first, becoming pale orange to orange gray (5, A-B, 2-4) when faded; margin exceeding lamellae by 1-2 mm, decurved, translucent-striate when moist; context up to 2 mm thick near the umbo, pale brown; taste sweet; odor pleasant and candy-like. *Lamellae*: narrowly adnexed to almost free, close to subdistant, 6 mm broad, 13 mm long, pale, brown at first, becoming pinkish; margin entire and concolorous. *Stipe*: 50-60 mm long, 1.5-2 mm broad at the apex; equal, terete; surface pruinose to flocculose at the apex, glabrous elsewhere; grayish orange to brownish orange (5, A-C, 4-5), paler at the apex; context stuffed then hollow.

Sporae 8-10 x 7-8.5 μ , average length 9.2 μ , average width 7.7 μ , L/D 1-2 μ (average 1.5 μ), ovate-angular, 4-6 sided, symmetrical. Basidia 31-45 x 9-12 μ , average length 37.7 μ , average width 10.5 μ , L/D 3.1-4.4 (average 3.6), clavate, 2-4 spored. Cheilocystidia and pleurocystidia absent. Pileal cuticle repent in tangential section with rare, more or less erect hyphae; terminal cells cylindro-clavate, 32-105 x 9-12 μ , with no external incrustations. Cuticle at the stipe apex with scattered clusters of clavate cylindro-clavate, colorless caulocystidia, 28-82 x 8-10 μ , average length 51.6 μ , average width 7 μ , L/D 3.1-8.2 (average 7.4); external incrustations absent. Lactifers absent. Clamp connections present at the base of the basidia, absent on the hyphae of the pileal cuticle, of the lamellae trama, and of the cuticle of the stipe apex.

Macrochemical Reactions: Guaiac, Guaiacol, Pyrogallol, Alpha-Naphthol, Selenium Dioxide, and PDAB were positive in all parts of the basidiocarp. All other reagents were not used.

Habit and Habitat: Scattered in leaf humus beneath Red Alder.

TYPE: WASHINGTON: Island Co.: Scattered in leaf humus beneath Red Alder, Fort Casey State Park, Whidbey Island, 2 Nov. 1967, Largent 3358 (HOLOTYPE: HSC).

Additional Material Studies: WASHINGTON: Island Co.: Largent 3355.

Nolanea fructufragrans can be recognized by its grayish brown pileus, pale brown lamellae, ovate-angular spores, caulocystidia, and the pleasant, candy-like odor. As far as we can tell, only two species of rhodophylloid fungi have a similar odor, *Rhodophyllus icterinus* (Fr.) Quél. and *R. ameides* (Berk. & Br.) Quél. The former differs from *N. fructufragrans* by having a pileus and stipe some shade of yellow, larger spores and no cheilocystidia; the latter differs by having a gray to brown stipe and pileus, a larger stipe (30-65 mm long and 3-5 mm broad at the apex) and larger spores (10-13 x 7.5-9 μ).

4. *Nolanea* (Fr.) Kummer em Largent & Benedict, Section *Staurospori* sect. nov.

Basionym: *Rhodophyllus* Quél., Section *Pascui* Romagn., Subsection *Staurospori* Romagn. Soc. Mycol. Fr. 53: 331. 1937.

Synonym: *Rhodophyllus* Quél., Subgenus *Nolanea* (Fr.) Quél. sensu Singer 1946, Section *Nolanea* Singer, Subsection *Staurospori* Romagn. Agaricales in Modern Taxonomy, p 691 (1961)

Sporae angulato-verrucosae vel stellato-angulatae. Typus *Rhodophyllus staurosporus* (Bres.)

J. Lange.

We feel the possession of prismatic or nodulose-angular basidiospores is sufficiently distinct to raise Romagnesi's subsection to the rank of section. As far as we can determine a Latin diagnosis has never been submitted for this category and a type species was not designated until 1962.

Type species: *Rhodophyllus staurosporus* (Bres.) J. Lange

a. *Nolanea staurospora* (Bres.) J. Lange var. *farinacea* var. nov.

Pileus griseo-brunneus, hygrophanus. Odor farinaceus. Vulcolae pigmento in hyphis cuticularibus. Lamellae albae. Sporae angulato-verrucosae vel stellato-angulatae.

Typum legit: D. L. Largent, n. 1597, Sulphur Creek, Campground, Mt. Baker National Forest, 20 Sept 1966. In herbario Humboldt State College conservatum.

Pileus: 15-45 mm broad, 4-20 mm high, broadly campanulate becoming broadly convex to plane; surface glabrous to the eye but with a "scum" of dark colored hyphae on the disc as seen with a dissecting microscope, hygrophanous; dark gray brown (5-6, E-F, 3-4) on the disc and light brownish gray to grayish brown to light yellowish brown (5-6, D-E, 2-5) elsewhere, fading to brownish orange to grayish orange (5, B-D, 2-4) with the disc often remaining darker; margin decurved becoming plane, even to irregularly lobed, at first translucent-striate becoming smooth; context up to 2 mm thick near the disc, whitish at first but with a "Pale Olive Buff" line beneath the cuticle; taste and odor farinaceus. *Lamellae*: narrowly adnate adnexed, in some almost free, narrow when young becoming moderately broad to broad, at first white to "Tilleul Buff" becoming pinkish ("Shell Pink" to "Avellaneous"); margin even and concolorous, at times becoming faintly reddish brown when bruised. *Stipe*: 40-85 mm

long, 2-4.5 mm broad at the apex, 2-7 mm broad at the base, equal to tapered from the base to the apex; terete but occasionally twisted and/or compressed and grooved; glabrous and with silvery, often agglutinated, superficial fibrils, then longitudinally striate; silvery white to pale orange to orange white (5-6, A-B, 1-3) at first, becoming light brown to dark yellowish brown (5, D-F, 4-5) from the base upwards when bruised or handled or when the superficial fibrils agglutinate; context stuffed then hollow, concolorous with the pileal trama.

Spores $10-13 \times 8-11.5 \mu$, average length 10.9μ , average width 9.9μ , L/D $0.0-4 \mu$ (average 1μ), ovate-angular, asymmetrical, prismatic or angular nodulose in side view, triangular in end view. Basidia $27-47 \times (8-)$ $9.5-14.2 \mu$, average length 30.6μ , average width 12.1μ , L/D $2.1-3.3$ (average 2.5), clavate, 2-4 spored. Cheilocystidia and pleurocystidia absent. Hyphae of the lamellar trama up to 15μ wide. Cuticle of the pileal disc a loosely entangled trichodermium, elsewhere repent in tangential section; terminal cells cylindro-clavate, $35-90 \times 8-13$ (-17) μ , average length 48μ , average width 9.1μ , L/D $3.5-10$ (-13.5) (average 5.3), with a vacuolar pigment; hypoderm subcellular with ovoid hyphae and numerous lactifers. Cuticle of the stipe apex repent in scalp section and with numerous lactifers; hyphae without any external incrustations. Clamp connections absent on the hyphae of the pileal cuticle, of the cuticle of the stipe apex, and of the lamellar trama, absent at the bases of the basidia and basidioles.

Macrochemical Reactions: All chemical tests were negative.

Microchemical Tests: Carminophilous granulation and metachromatism with lactic acid and cotton blue, lactophenol and cotton blue, scarlet red and cresyl blue all negative. Picroformol of Holland test: positive for vacuolar pigmentation.

Habit and Habitat: Solitary among mosses beneath Devil's Club, ferns, or Vine Maple, near Mountain Hemlock and Western Red Cedar in mixed conifer-hardwoods.

TYPE: WASHINGTON: Snohomish Co.: Sulphur Creek Campground, Mt. Baker National Forest, 20 Sept 1966, *Largent* 1597 (HOLOTYPE: HSC).

Additional Material Studied: IDAHO: Valley Co.: *Largent* 357, 453, 572. WASHINGTON: King Co.: *Largent* 1306, 1710, 1851, 3142. Lewis Co.: *Largent* 1355. Pierce Co.: *Largent* 1656, 1673. Snohomish Co.: *Largent* 1279, 1295.

The distinctive features of *Nolanea stauropora* var. *farinacea* include its gray brown hygrophanous pileus, dark scum of hyphae on the pileal disc caused by the loosely entangled trichodermium, vacuolar pigmentation in the hyphae of the pileal cuticle, white lamellae, farinaceous odor, and angular-nodulose or stellate-angular spores.

Our species agree with the description of *Rhodophyllum stauroporus* sensu Orton and sensu Kühner & Romagnesi. Orton (1964) considers all forms of *Rhodophyllum stauroporus* to have a farinaceous odor whereas Kühner & Romagnesi (1953, 1954) consider only certain varieties to have a similar odor. These investigators identified their collections as *Rhodophyllum stauroporus* on the basis of the description given by J. Lange in 1936; J. Lange identified his collections as *Nolanea stauropora* on the basis of the description given by Bresadola in 1929. However, Bresadola's description specifically states "inodora and insapora" (Bresadola, 1927-1933). Therefore, we feel *Nolanea stauropora* var. *stauropora* should be restricted to those forms of this species without an odor or a taste and var. *farinacea* should be used for those forms with a farinaceous odor and taste.

Our variety is similar to *Rhodophyllum stauroporus* var. *typicus* Romagn. and to var. *platyphyllum* Favre & Romagn., but differs from the former by having larger spores and from the latter by having white lamellae, a larger pileus, and nonprotruding gills. *Rhodophyllum stauroporus* var. *rickenii* (Romagn.) Romagn. differs from our variety by having a mild odor and taste. *Rhodophyllum stauroporus* var. *obscurior* Romagn. and var. *subrugosus* Romagn. should be considered *nomen nuda* due to the absence of Latin diagnoses; their descriptions lack sufficient detail to make a comparison with our species. *R. stauroporus* var. *argentea* Killern, var. *luxurians* Brs., var. *minor* Bres., and var. *alpina* Bres. are not described adequately. Other species that are closely related to *Nolanea stauropora* as listed below:

(1) *Rhodophyllum xylophilus* Lange has smaller spores ($10 \times 8.5 \mu$), a pileus up to 10 mm broad, and a lignicolous habitat.

(2) *Rhodophyllum pinnuus* Romagn. has larger spores ($14-16 \times 10-15 \mu$), a more robust stature (stipe 100-150 mm long), and a weak odor and taste.

(3) *Entoloma subquadratum* Hesler has a lighter pileus, mild to subacidulous taste and odor and smaller spores ($8-10 \times 6.5-7.5 \mu$).

b. *Nolanea stauropora* (Bres.) J. Lange var. *incrustata* var. nov.

Hyphae cuticulares pilei externe annulari-incrustatae.

Typum legit D. L. Largent, n. 2888, Clallam Co.: Washington, 2 Oct 1967; in herbario Humboldt State College conservatum.

Hyphae of the pileal cuticle and pileal trama with external ring-like incrustations.

Microchemical reactions:

Pyrogallol positive in all parts, all other tests negative in all parts.

Habit and Habitat: Solitary to scattered among *Sphagnum* beneath Western Red Cedar in a coniferous forest.

TYPE: WASHINGTON: Clallam Co.: Scattered in mossy humus beneath Western Red Cedar, Trail to Ozette Reservation, Olympic National Park, 2 Oct 1967, *Largent* 2888 (HOLO-

TYPE: HSC).

With the exception of the external incrustations, this species is similar in most other respects to *N. staurospora* var. *farinacea* Largent and Thiers.

Summary

Four new sections, *Endochromonema*, *Holoconiotae*, *Cosmeoexonema* and *Staurospori*, are proposed for the genus, *Nolanea* (Fr.) Kummer em Largent & Benedict. Three new species, *Nolanea holoconiota*, *N. bicoloripes*, *N. fructufragrans*, and two new varieties, *Nolanea staurospora* var. *farinacea*, and var. *incrustedata*, are proposed. Detailed descriptions of sections, species, and infraspecific taxa are provided.

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Geographic Distribution of Micropezidae in the Western United States (Diptera)²

Merritt and James (1972) have presented a review of the dipterous family Micropezidae, as it occurs in the Rocky Mountains and Pacific Coast states. This work concerns particularly the fauna of California, but all western species are treated in the keys and discussion. Geographical records for California are given in detail.

The purpose of this paper is to present the distributional data, in summary form, of each species for the western states other than California.

Subfamily Calobatinae
Genus *Cnodacophora* Czerny
Cnodacophora nasoni (Cresson)

Calobata nasoni Cresson, 1914, Entomol. News, 25: 459. Type ♂, Algonquin, Illinois (Acad. Nat. Sci. Phila., no 6078).

Geographic Range.—Alaska, Washington, and Alberta to Quebec, south to Colorado, Illinois, and New York.

Records.—COLORADO: Boulder Co., Longmont. IDAHO: Bear Lake Co., St. Charles Cyn., Wasatch Range. Latah Co., Viola. OREGON: Deschutes Co., Deschutes R. near Redmond. Douglas Co., Vincent Cr. Rd., 3 mi. E. Smith River Jct. UTAH: Cache Co., Blacksmith Fork Cyn.; Logan Cyn. Duchesne Co., Duchesne; Altonah. Morgan Co., Strawberry Valley. Rich Co., Laketown. WASHINGTON: Pacific Co., Nahcotta. Whatcom Co., Marietta. Whitman Co., Pullman. WYOMING: Platte Co., Wheatland; Yellowstone Nat. Pk. Late April to late August.

Genus *Compsobata* Czerny
Subgenus *Compsobata* Czerny
Compsobata (*Compsobata*) *univittata* (Walker)

Calobata univittata Walker, 1949, List Insects British Museum, Dept., 4: 1049. Type?, New York, and St. Martin's Falls, Albany River, Hudson Bay [British Museum (Natural History)]. Geographic Range.—British Columbia to Quebec, south to California, New Mexico, Illinois, Maryland.

Records.—COLORADO: Boulder Co., Longmont. Larimer Co., Fort Collins. IDAHO: Boundary Co., 1 mi. N. Copeland. Latah Co., Moscow; Moscow Mtn.; Laird Park; Harvard. Lemhi Co., Salmon. Nez Perce Co., Lewiston. NEVADA: Washoe Co., Sparks; Verdi. OREGON: Columbia Co., Scappose. Hood River Co., Hood River. Jackson Co., Squaw Lake. Klamath Co., 10 mi. N.E. Bly, Long Creek; Wood River Spring. UTAH: Boxelder Co., Brigham. Cache Co., Logan Canyon; Blacksmith Fork Cyn. Weber Co., Huntsville. WASHINGTON: Pierce Co., Puyallup. Spokane Co., Valleyford. Whitman Co., Pullman, Asotin Cr.; Lyle Grove—Pullman.

Late April to mid-August; shaded marsh.

Subgenus *Trilophyrobata* Hennig
Compsobata (*Trilophyrobata*) *jamesi* Merritt

Compsobata (*Trilophyrobata*) *jamesi* Merritt, 1971, Pan-Pac. Entomol. 47: 179. Type ♂, Nahcotta, Pacific County, Washington (Washington State University).

Geographic Range.—Washington.

Records.—WASHINGTON: Pacific Co., Nahcotta. Whatcom Co., Marietta. May and June; coastal area.

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Compsobata (Trilophyrobata) microfulcrum (James)

Paracalobata microfulcrum James, 1946, Entomol. News, 57: 129. Type ♂, Divide, Teller County, Geographic Range.—Colorado, Arizona.

Colorado (Colorado State University).

Records.—ARIZONA: Apache Co., Greer, 10 mi. S.W.; Phelps Bot. Area. COLORADO: Teller Co., Florissant. June and July.

Compsobata (Trilophyrobata) mima (Hennig)

Trepidaria mima Hennig, 1936, Konowia, 15: 134. Lectotype ♂ (designation by Cresson), Electra Lake, La Platte County, Colorado (Amer. Mus. Nat. Hist.).

Geographic Range.—British Columbia to Saskatchewan, south to California and Colorado.

Records.—COLORADO: El Paso Co., Colorado Pass. Gilpin Co., Tolland. Jackson Co., N. of Grizzly Cr. Camp; Walden. Larimer Co., Longs Peak Inn; Cameron Pass; Lake Agnes near Cameron Pass. La Plata Co., Electra Lake, about 37° 33' N. 107° 48' W. 8400 ft. IDAHO: Bear Lake Co., Mud Lake; St. Charles Cyn., Wasatch Range. Bonner Co., Granite L., Bonneville Co., 9.4 mi. N. Swan Valley. Boundary Co., Kalispel Bay. Camas Co., Rock Cr. R.S. Caribá Co., Wayan. Cassia Co., Rock Cr. R.S.; Minidoka N.F. Clearwater Co., Elk River. Custer Co., Challis; Stanley Basin; 5 mi. W. Stanley; Whitney. Elmore Co., Lake Comas. Franklin Co., Franklin; Preston. Fremont Co., Swan Lake. Idaho Co., Ferdinand; Lolo Pass. Latah Co., Harvard; Moscow Mt.; Troy—5 mi. N. Lemhi Co., 5 mi. S. Salmon. Valley Co., 3.3 mi. N.W. Cascade; 2.2 mi. E. Lick Cr. Summit; New Meadows. MONTANA: Lake Co., Swan Lake—Marsh. Lincoln Co., Thompson. Yellowstone N.P., Yellowstone Lake. NEVADA: Elko Co., Lamoille; Wells. OREGON: Baker Co., Haines. Clackamas Co., Mt. Hood. Crook Co., Ochoco Pass. Deschutes Co., Redmond; Tumalo; Tumalo St. Park. Douglas Co., Diamond Lake, 15 mi. S.W. Grant Co., Prairie City; Seneca. Klamath Co., Eagle Ridge—Klamath Lake; Crater Lake; Crater Lake—Sphagnum bog; Mare's Egg Spring; Klamath Falls on saw grass; Meryl Cr. 7 mi. N.W. of Bly; 3 mi. S.E. of Odell Lk.; Sprague River—5 mi. E. of Bly; Crooked Cr.; Wood River Spring. Lake Co., Chewaucan River Dam Site. Union Co., 3 mi. S.E. of Spout Springs; Tollgate Pass; North Powder. Wallowa Co., Enterprise. Wheeler Co., Mt. Creek. UTAH: Cache Co., Benson; Logan Canyon; Monte Cristo; Providence; Logan; Logan—White Pine Lake; Smithfield; Hyde Park; Amalga; Elk Park Cr.; Blacksmith Fork Canyon; Wellsville; Paradise; Logan Park Inn. Carbon Co., Gooseberry Lake—Clear Cr. Canyon. Daggett Co., Manila. Duchesne Co., Mt. Home; Cub Cr., Unita Mts.; Wolf Cr. Pass. Emery Co., Huntington Canyon; Castle Dale. Kane Co., Glendale; Kanab Cr.; Duck Cr. Camp. Millard Co., Willard Basin. Piute Co., Circleville. Rich Co., Laketown; Garden City. San Pete Co., Indianola. Summit Co., Oakely; Daniel's Canyon; Peoa, Soldier Summit; Gargoza; Kimballs. Uintah Co., Vernal. Utah Co., Francis; Linden; Payson. Wasatch Co., Heber; Meadow Spring; Wallsburg; Midway. Wayne Co., Torrey. Weber Co., Eden. WASHINGTON: King Co., North Bend. Spokane Co., Diamond Lake. Whitman Co., Pullman; Lyle Grove, Pullman. WYOMING: Teton Co., Jenny L. Gr., Teton N.P. Yellowstone National Park, W. Yellowstone; Old Faithful; Yellowstone L., Geyser; Indian Cr.; Madison Jct.; Turbid Lake.

Late April to November; marsh and meadow habitats at altitudes up to 10,000 feet.

Compsobata (Trilophyrobata) pallipes (Say)

Calobata pallipes Say, 1823, J. Acad. Nat. Sci. Philadelphia, 3: 97. Type, Missouri; lost.

Geographic Range.—Alaska, Alberta to New Brunswick, south to Nevada, and New Jersey.

Records.—COLORADO: Boulder Co., Boulder; Lodge. Larimer Co., Pingree. Weld Co., Roggen. June and July.

Subfamily Micropezinae

Genus *Micropeza* Meigen

Subgenus *Micropeza* Meigen

Micropeza (Micropeza) abnormis Cresson

Micropeza abnormis Cresson, 1938, Entomol. News, 49: 72. Type ♂, Baboquivari Mountains, Pima County, Arizona (Univ. of Kans.).

Geographic Range.—Known only from Arizona.

Records.—ARIZONA: Pima Co., Santa Rita Mts.; Molino Basin; Santa Catalina Mts. Santa Cruz Co., Ruby; Madera Cyn.; Sycamore Cyn. near Ruby; Molina Basin; Santa Catalina Mts.; Calabasas, 6 mi. W. Nogales.

July and August.

Micropeza (Micropeza) ambigua Cresson

Micropeza turcana ambigua Cresson, 1908, Trans. Amer. Entomol. Soc., 34: 3. Lectotype ♂ (designation by Cresson) Cloudcroft, New Mexico (Acad. Nat. Sci. Phila., no. 6011).

Geographic Range.—New Mexico, Arizona, California.

Records.—ARIZONA: Coconino Co., Grand Canyon—7000 ft.; Oak Creek Cyn. NEW MEXICO: Otero Co., Cloudcroft; Highrolls. Sandoval Co., Jemez Mts.

Late May to mid-July.

Micropeza (Micropeza) atra Cresson

Micropeza atra Cresson, 1938, Entomol. News, 49: 74. Type ♀, Flagstaff, Coconino County, Arizona (U.S. Nat. Mus., no. 27059).

Geographic Range.—Arizona, New Mexico.

Records.—NEW MEXICO: Sandoval Co., Jemez Mts. UTAH: Iron Co., Bear Valley. May and June.

Micropeza (Micropeza) compar Cresson

Micropeza compar Cresson, 1938, Entomol. News, 49: 73. Type ♂, Huachuaca Mountains, Arizona (Univ. of Kans.).

Geographic Range.—Arizona, New Mexico.

Records.—ARIZONA: Apache Co., 5 mi. S. McNary. Cochise Co., Chiricahua Mts.; Flys Peak, 85-9700 ft.; S.W. Res. Station, 5 mi. W. Portal; Paradise. Coconino Co., Manzanita Cpgd; Oak Creek Cyn.; Williams, Alt. 7000 ft. Graham Co., Graham Mt.; Pinecrest. Greenlee Co., 22 mi. N. Clifton. Navajo Co., Whiteriver. Pima Co., Marshall Gulch; Sta. Catalina Mts.; Rincon Mts., 7500 ft. Pinal Co., Pinal Mts. Yavapai Co., Mingus Mt.; 1 mi. S.W. Mingus Mt. NEW MEXICO: Carton Co., 87 mi. N.W. Silver City, 5900 ft. Taken on *Robinia neomexicana*, and *Apocynum* sp. (Indian hemp); June and July; mountain areas.

Micropeza (Micropeza) lineata Van Duzee

Micropeza lineata Van Duzee, 1926, Pan-Pac. Entomol., 3: 2. Type ♂, Utah Lake, Lehi, Utah County, Utah (Calif. Acad. Sci., no. 1879).

Geographic Range.—Alberta to Manitoba, south to California, New Mexico and Nebraska.

Records.—ARIZONA: Cochise Co., Huachuca Mts.; Chiricahua Mts.; Ramsey Cn. Coconino Co., Imperial; Flagstaff. Navajo Co., Taylor. Yavapai Co., Mingus Mt. COLORADO: Baca Co., 20 mi. S. of Walsh. Bent Co., Las Animas. Boulder Co., Boulder; 6 mi. N. of Boulder. Chaffee Co., Salida. Larimer Co., Ft. Collins. Moffat Co., Maybell. Pueblo Co., Pueblo. IDAHO: Bear Lake Co., Dingle. Elmore Co., Hammett. Franklin Co., Whitney; Preston. Gooding Co., Bliss. Jefferson Co., 4 mi. E. Terreton; 7 mi. W. Fort Hall. Nez Perce Co., Lewiston. Twin Falls Co., Salmon Crk., 5 mi. S. Castleford. MONTANA: Gallatin Co., Three Forks. Park Co., Gardiner. NEW MEXICO: Otero Co., Highrolls. UTAH: Beaver Co., Beaver. Cache Co., Logan; Wellsville; Millville; Hyrum. Daggett Co., Antelope; Manila. Davis Co., Farmington. Duchesne Co., Roosevelt; Indian Cyn. Millard Co., Delta. Rich Co., Garden City; Greendale. Salt Lake Co., Murray. Sevier Co., Monroe; Elsinore. Tooele Co., Ophir Mts. Utah Co., American Fork; Spanish Fork; Provo; Lehi. Washington Co., St. George. Weber Co., Kanesville; Ogden; Hooper; Plain City. WASHINGTON: Whitman Co., Kamiak Butte. WYOMING: Carbon Co., Fremont Co., nr. Lander; Little Wind R. Niobrara Co., Lance Cr.; Buck Creek; 40 mi. N. Lusk. Late May to mid-August.

Micropeza (Micropeza) nitidor Cresson

Micropeza nitidor Cresson, 1936, Trans. Amer. Entomol. Soc., 44: 319. Type ♀, Bear Wallow, Santa Catalina Mts., Arizona (Amer. Mus. Nat. Hist.).

Geographic Range.—Known only from Arizona.

Records.—ARIZONA: Cochise Co., Chiricahua Mts., 8000 ft. Graham Co., Arcadia For. Cmp.; Pinaleno Mts., 6700 ft. Pima Co., Catalina Mts.; Mt. Lemmon, Sta. Catalina Mts., 9000 ft.; Mud Springs, Sta. Catalinas, 32° 23' 3" N., 110° 45' W.; 6500 ft. Alt.; Bear Wallow, Sta. Catalina Mts. June and July; mountain areas.

Micropeza (Micropeza) setaventris Cresson

Micropeza setaventris Cresson, 1936, Entomol. News, 49: 74. Type ♂, Fort Duchesne, Utah (Acad. Nat. Sci. Phila., no. 6536).

Geographic Range.—Utah, Colorado and North Dakota, south to Arizona and New Mexico.

Records.—ARIZONA: Apache Co., Springerville. Navajo Co., Whiteaver. COLORADO: Las Animas Co., Stonewall. NEW MEXICO: Sandoval Co., Jemez Springs. San Miguel Co., Pecos. UTAH: Box Elder Co., Brigham Cyn. Cache Co., Smithfield; Avon; Logan Cyn.; Providence. Salt Lake Co., Murray. Sevier Co., Nibley. Weber Co., Hooper. Late June to mid-August.

Micropeza (Micropeza) turcana Townsend

Micropeza turcana Townsend, 1892, Trans. Kans. Acad. Sci., 13: 136. Lectotype ♂ (designation by Cresson) Turkey Tanks, Coconino County, Arizona (Univ. of Kans.).

Geographic Range.—Alberta to Manitoba, south to Arizona and Kansas.

Records.—ARIZONA: Coconino Co., 8 mi. N.E. Flagstaff. COLORADO: Baca Co., 28 mi. S. of Walsh. Weld Co., Roggen. IDAHO: Fremont Co.; St. Anthony, sand dunes. UTAH: Grand Co., Castle Valley. Taken on *Cleome serrulata*; May to July.

Micropeza (Micropeza) unca Merritt

Micropeza (Micropeza) unca Merritt, 1971, Pan-Pac. Entomol. 47: 181. Type ♂, Davis, Yolo County, California (Univ. of Calif., Davis).
Geographic Range.—Known only from California.

Micropeza (Micropeza) ventralis Cresson

Micropeza ventralis Cresson, 1930, Trans. Amer. Entomol. Soc. 56: 356. Type ♂, Tacubaya, Distrito Federal, Mexico (U.S. Nat. Mus., no. 43149).
Geographic Range.—Mexico (D.F.), Arizona.
Records.—MEXICO: Tacubaya, Distrito Federal.

Subgenus *Neriocephalus* Enderlein

Micropeza (Neriocephalus) bisetosa Coquillett

Micropeza bisetosa Coquillett, 1902, J. New York Entomol. Soc. 10: 177. Type ♂, Prescott, Arizona (U.S. Nat. Mus., no. 6626).
Geographic Range.—Arizona, New Mexico.
Records.—ARIZONA: Cochise Co., Sunnyside Cyn., Huachuca Mts. Pima Co., Santa Rita Mts.; Madera Cyn.; Bear Wallow; St. Catalina Mts., 32° 23.3' N. 110° 44' W. Santa Cruz Co., Ruby; Tumacacori Mt.; W. Sl. Patagonia Mts. Yavapai Co., Prescott. NEW MEXICO: Grant Co., Silver City.
July to September; mountain areas.

Micropeza (Neriocephalus) californica Van Duzee

Micropeza californica Van Duzee, 1926, Pan-Pac. Entomol., 3: 1. Type ♀, Palm Springs, Riverside County, California (Calif. Acad. Sci., no. 1878).
Geographic Range.—Known only from California.

Micropeza (Neriocephalus) ruficeps Wulp

Micropeza ruficeps Wulp, 1897, Biologia Centrali-Americana, Dipt. 2: 365. Type ♀, Northern Sonora, Mexico [British Museum (Natural History)].
Geographic Range.—Mexico, California, Arizona.
Records.—ARIZONA: Cochise Co., Portal, 1 mi. S.; Cave Cr. Ranch; Chiri Mts. 5000 ft.; S. Fork, Cave Cr.; S.W. Res. Sta.; 5 mi. W. Portal. Pima Co., Sabino Cyn.; 8 mi. N. Vail; Htchk. Hwy.; Mi. 4, Catalina Mts.; Lower Sabino Cyn.; Santa Catalina Mts.; Tucson; Madera R.S. Sta., St. Rita Mts.; E. Slope Coyote Mts.; 1/2 mi. N. Mendoza Cyn. Santa Cruz Co., Patagonia. Taken on *Franseria deltoidea*.
May to August.

Micropeza (Neriocephalus) stigmatica Wulp

Micropeza stigmatica Wulp, 1897, Biologia Centrali-Americana, Dipt. 2: 366. Cotypes, Mexico, several localities [British Museum (Natural History)].
Geographic Range.—Arizona, New Mexico, Kansas, Texas, south to Argentina.
Records.—ARIZONA: Cochise Co., Douglas; San Bernardo Ranch; Bowie; San Simeon. Gila Co., Winkelman. Graham Co., Thatcher; Indian Hot Springs; Stafford. Greenlee Co., Duncan. Maricopa Co., Tempe. Pima Co., Tucson; Sahuarita; Continental. Santa Cruz Co., Amado; Tubac. Yavapai Co., Cottonwood. NEW MEXICO: Hidalgo Co., 1 mi. S. Rodeo; 18 mi. N. Rodeo. Taken on corn and alfalfa.
March to late August.

Subfamily *Taeniapterinae*

Genus *Taeniaptera* Macquart

Taeniaptera lasciva (Fabricius)

Musca lasciva Fabricius, 1798, Entomologia Systematica, Suppl., 564. Type (sex?), French Gniaia (Location of type unknown).
Geographic Range.—Lower California, Texas, Georgia, Florida, Neotropical.
Records.—TEXAS: Cameron Co., Brownsville.

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Plant Moisture Stress Patterns in *Eurotia lanata* and *Atriplex confertifolia*²

Introduction

There are *a priori* reasons to expect that plants might have different tolerances to varying degrees of water stress and that their natural distribution might be a reflection of their relative abilities to withstand low water potentials. As a case in point, Waring's (1970) pressure bomb measurements of plant moisture stress have greatly helped to explain the distribution of mesophytes in southwestern Oregon. If such measurements are useful in subhumid environments, it is logical that they may be even more valuable in assessing site differences and explaining the distribution of desert species.

The effects of soil moisture on xerophyte growth are difficult to interpret in deserts where the additional influence of salinity on total soil moisture stress exists. Furthermore, it recently has been shown that much of the growth of desert shrubs occurs when soil moisture is below the permanent wilting percentage for agronomic species (Chew and Chew, 1965; Gasto, 1969).

Water status measurements in the plant seem to be a more direct assessment of ecological relationships than soil moisture data. The ease of using the pressure bomb, the close correlation of bomb data with water potential (Wiebe *et al.*, 1970; Detling and Klikoff, 1971), and the physiological relevance of water potential encouraged us to test the utility of this approach in helping to explain plant distribution in a cool-desert situation. We did so by measuring plant moisture stress in *Eurotia lanata* (Pursh.) Moq. (winterfat) and *Atriplex confertifolia* (Torr. & Frem.) Wats. (shadscale) during two growing seasons and correlating these data with phenology and climatic conditions.

Methods

Internal moisture stress was measured by the apparatus designed by Waring and Cleary (1967). The results are expressed, for convenience, in positive atmospheres, rather than a negative measurement as used by Scholander *et al.* (1965) and Pierpont (1967).

The studies were made several km north of the Great Salt Lake in Curlew Valley, northwestern Utah, using plants from three different stands, all at the 1350 m contour.

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² Approved as Journal Paper 1133 of the Utah Agricultural Experiment Station.

Site 1. *E. lanata* community in the valley bottom.

Site 2. Mixed *E. lanata* and *A. confertifolia* community, about 0.2 km to the west of site 1.

Site 3. *A. confertifolia* community about 0.2 km to the west of site 2.

The vegetation and soil chemical and physical characteristics of this study area have been described by Gates *et al.* (1956) and Mitchell *et al.* (1966).

Data were collected from April-November, 1968 and from March-October, 1969, usually at weekly intervals. An exception was the six-week period during September to mid-October 1969 when data were missed because of illness of the senior author. On each occasion, 10 plants from the *E. lanata* stand, 10 plants from the *A. confertifolia* stand, and five plants of each species from the mixed stand were measured. Mature plants were selected at random, and their general condition was noted. The samples were taken between 10:00 a.m. and 2:00 p.m. each day. Standards of measurement established by Scholander *et al.* (1965) and Waring and Cleary (1967) were followed.

Diurnal pressure bomb readings were made in May, 1969, in order to assess the degree of fluctuation in plant moisture stress during the course of a day. The measurements were made at hourly intervals during the day and at suitable intervals during the evening. Only plants from the monospecific stands were measured.

Climatic data on rainfall, air temperature, relative humidity, wind speed, and radiation were collected from a nearby weather station. Soil moisture measurements during 1968 were made with a neutron probe.

Results

Mean plant moisture stress values for each species and stand are depicted in Figures 1 (1968) and 2 (1969). Diurnal moisture values for May 12-13, 1969 are recorded in Table 1.

TABLE 1. Diurnal plant moisture stress variation in *Eurotia lanata* and *Atriplex confertifolia* at Curlew Valley, May 12-13, 1969.

		Plant Moisture Stress (atm) Mean of Ten Plants	
	Time of Day	<i>E. lanata</i>	<i>A. confertifolia</i>
(sunset)	1700 hours	27.7	32.7
	1800	29.7	27.8
	2030	27.0	22.3
	2230	16.5	22.4
(sunrise)	0603	20.3	17.1
	0800	22.5	22.4
	0900	30.0	22.8
	1000	31.0	30.0
	1100	32.5	29.3
	1200	32.4	33.1
	1300	32.8	27.6
	1400	30.9	28.0

Growing season rainfall and weekly maximum temperatures, the most relevant climatic parameters, are recorded in Figures 1 and 2. Soil moisture data are found in Table 2. Phenological sequences are shown in Table 3.

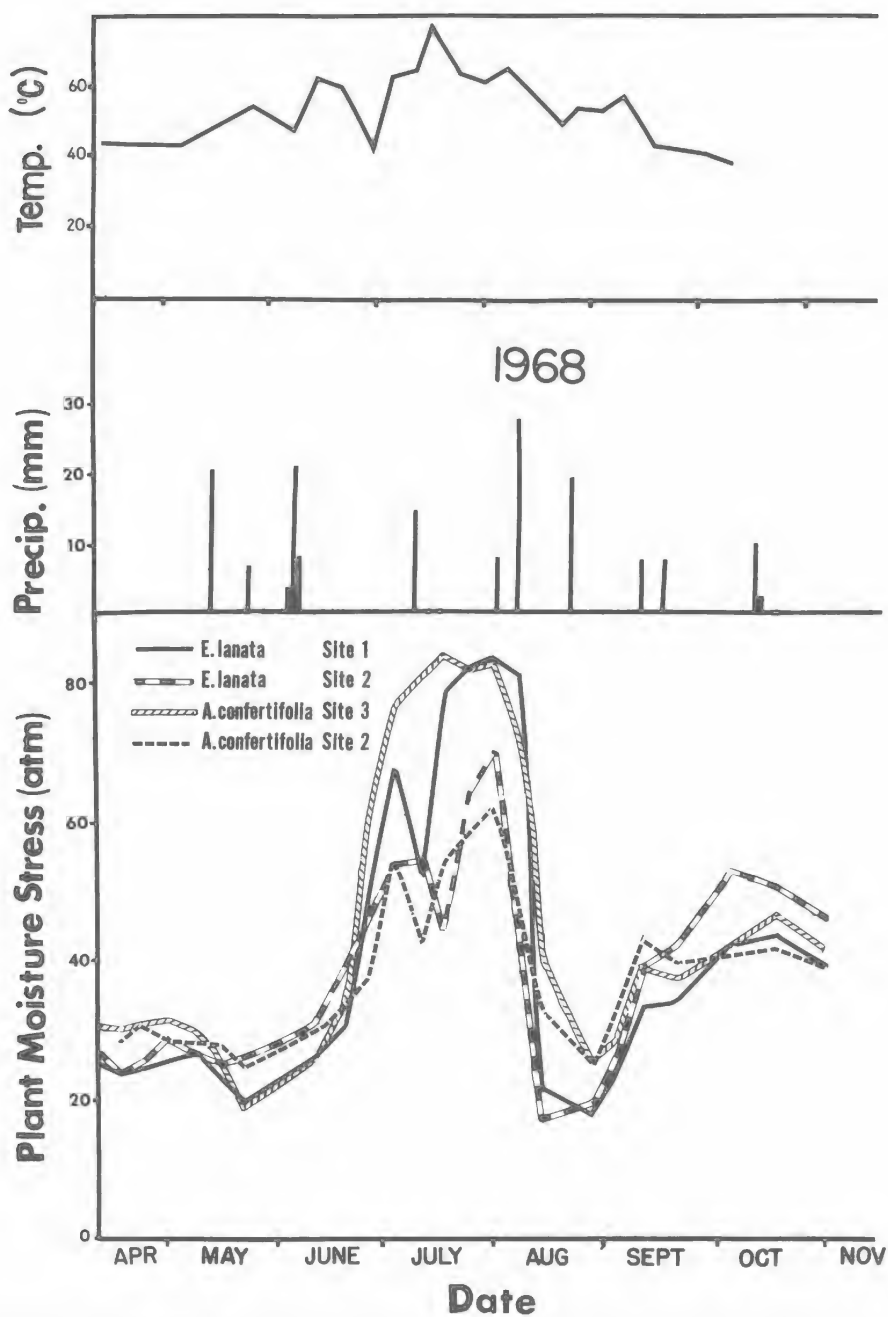


Figure 1. Trends of mean plant moisture stress taken during the 1968 growing season with concomitant precipitation events and weekly maximum temperatures.

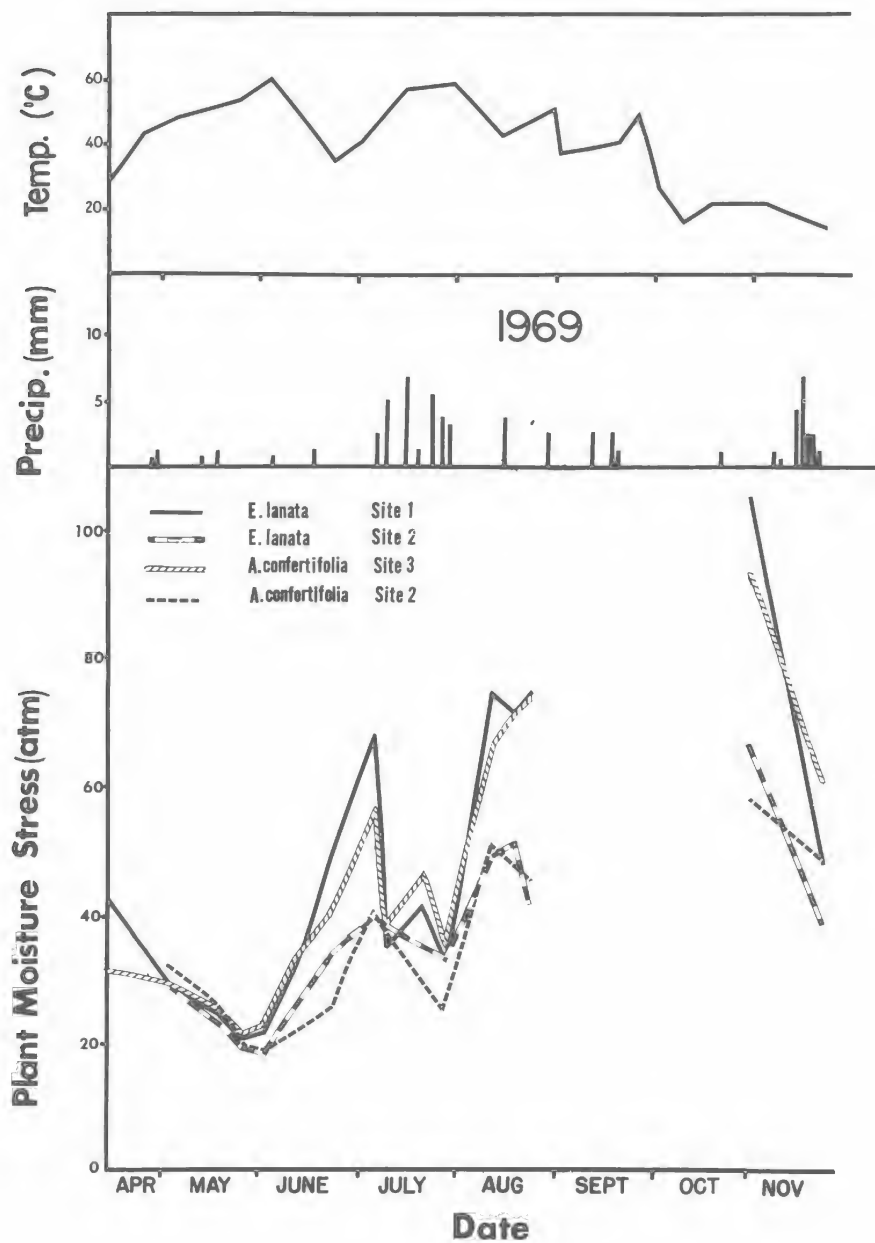


Figure 2. Trends of mean plant moisture stress taken during the 1969 growing season with concomitant precipitation events and weekly maximum temperatures.

TABLE 2. Soil moisture data from three stands at Curlew Valley, 1968.

		Soil Moisture % by Weight (upper 15 cm)		
Date		Site #1 <i>E. lanata</i> Stand	Site #2 Mixed Stand	Site #3 <i>A. confertifolia</i> Stand
April	12	11.4	11.4	16.5
	20	10.7	10.0	14.5
	27	9.4	9.0	12.5
May	3	8.2	6.4	10.9
	10	5.6	4.8	9.2
	17	12.3	12.7	19.5
	24	8.4	9.1	14.7
June	20	7.4	6.3	9.1
July	4	3.3	3.1	5.9
	26	2.7	2.7	4.5
Aug.	13	10.2	10.6	14.2
Sept.	1	9.3	8.9	12.5
	19	6.6	7.6	8.6

TABLE 3. Phenology of *Eurotia lanata* and *Atriplex confertifolia* at Curlew Valley, 1968-1969.

		<i>Eurotia lanata</i>	
1968 Date		1969 Date	
3/0-3/16	Dormant	-3/14	Dormant
3/21-3/30	Vegetative buds swelling	3/14-4/4	Vegetative buds swelling
4/6-5/4	Twigs elongating	4/4-4/19	Twigs elongating
5/11-5/18	Floral buds developing	4/20-5/10	Floral buds developing
5/25-6/14	Flowers opening	5/5-6/3	Flowers opening
6/21-8/9	Fruit developing	5/24-7/24	Fruit developing
8/23-9/6	Fruit developing; new growth after fall rains	8/4-9/16	Fruit dissemination
10/5	Fruit dissemination, some twig elongation	9/23	Fall dormancy
11/9	Semi-dormant		
		<i>Atriplex confertifolia</i>	
3/9-3/16	Dormant	-3/29	Dormant
3/21-4/6	Vegetative buds swelling	3/29-4/4	Vegetative buds swelling
4/13-5/4	Twigs elongating	4/4-4/19	Twigs elongating
5/11-5/25	Floral buds developing	4/19-5/5	Floral buds developing
6/1-6/14	Flowers opening	5/10-6/3	Flowers opening
6/21-8/9	Fruit developing	6/9-7/17	Fruit developing
8/23-9/6	Fruit developing; new growth after fall rains	7/24-9/23	Fruit dissemination
10/5	Fruit dissemination, swelling of vegetative buds	9/30	Fall dormancy
11/9	Some elongation of fall twigs		

Discussion

Plant moisture stress data for *E. lanata* and *A. confertifolia* during 1968 (see Figure 1) show a definite correlation with seasonal changes in temperatures and rainfall. The highest values for both species in all stands occurred in July and August when the maximum temperatures for the year were recorded. The lowest values for both species in all stands occurred in May and the latter part of August, following 19.3 mm of rain in May and over 50.0 mm in August. At the onset of the growing season in early spring, all moisture stress values were relatively low and rose to a peak in summer during the period of flowering and fruiting (see Table 3). They decreased after the early fall rains, when new vegetative growth appeared, and rose again during the dry part of the fall. Almost every depression in Figure 1 can be accounted for on the basis of rain. Heavy rainfall generally resulted in reduced plant moisture stress, but storms of 8 mm or less had little effect on plant moisture stress. The storm of July 11 may have failed to depress the plant moisture stress at Site #3 because of less effective moisture infiltration into the saltier, finer-textured surface soils rooting this community (Gasto, 1969). None of the sites is more than 0.4 km apart at the same elevation, so greatly different rainfalls are unlikely.

Plant moisture stress data collected in 1969 also show a definite correlation with seasonal progressions of temperature and phenology as altered by rainfall. If the 1968 data are typical, it is likely that peak stresses occurred during the unseasonably hot and dry period of September and early October, 1969. Again, the least plant moisture stress for both species in all stands occurred in the late spring after heavy rainfall.

The plant moisture stress values recorded in this paper compare favorably with Scholander *et al.* (1965) who measured a negative sap pressure value of -80 atm for *Larrea tridentata*, and a recently reported plant moisture stress value of -128 atm for *Atriplex obovata* (Branson *et al.*, 1969). Detling (1969) recorded maxima of approximately -85 bars for *Suaeda fruticosa* and *S. depressa* at a slightly lower elevation along the southern shore of the Great Salt Lake.

Table 1 shows that both *E. lanata* and *A. confertifolia* vary considerably in moisture stress during a 24-hour period. On May 12, 1969, both species showed increases in plant moisture stress until sunset, when stress decreased, and reached a minimum sometime during the night. After sunrise on May 13, plant moisture stress gradually increased and reached a maximum about noon. Plant moisture stress values varied only slightly between 9:00 a.m. and 2:00 p.m. Readings were discontinued at 2:00 p.m. due to rain.

The results indicate that plant moisture stress in both species follows an expected pattern of increase to a maximum sometime during the early or later afternoon. The values decrease before sunset to a minimum during the night and rise again after sunrise. Plant moisture stress, at least during this period of the year, varies comparatively little during the part of the day when the weekly readings were collected. Unless a daily minimum value is required, this system of data collection seems satisfactory.

It is disappointing that the difference in distribution pattern between *E. lanata* and *A. confertifolia* in this study situation cannot be explained by data collected on plant moisture stress. Both species show similar patterns of variation in moisture stress, although *E. lanata* in the monospecific stand displayed more over-all variation

than *A. confertifolia* in its monospecific stand. When both species growing in a mixed stand were measured, they also showed a similar pattern of variation. Moreover, more variation occurs between samples of a species in mixed and monospecific stands than between the two species. The only thing that can be said with confidence is that the site conditions of the mixed stand were associated with less plant tissue moisture tension than that of the monospecific stands. The variability of the data makes statistical analysis of questionable value. Coefficients of variation for both species at all sites ranged from 13.8 to 22.1 percent from the driest to wettest periods of the growing season.

We conclude from the literature that a decrease in soil moisture and/or an increase in salinity of the soil will cause a corresponding decrease in plant water potential (increased plant tissue moisture tension) (Slayter 1967). The soil in which *A. confertifolia* was rooted had higher moisture content and soil salt content (Gasto, 1969), yet these plants showed less moisture tension than the *E. lanata* rooted in soil with lower moisture (Table 2). Detling (1969) had similar difficulty trying to explain the differing habitats of two *Suaeda* species on the basis of plant tissue moisture tension.

It is possible that halophytes are not amenable to this approach because of unique salt metabolism and occurrence in soils of differing soil moisture tension characteristics from that of glycophytes. Another possibility is that the sites studied have species-to-site relationships which are so far removed from pristine conditions that the present distribution of plants could be mostly a reflection of disturbance. Although the study area has not been grazed by domestic animals for the last eight years the area was grazed heavily for the bulk of the previous century. Some ecophysiological differences could be minor or indeterminate until competition reestablishes the species into their quasi-original niche separation. Research is currently underway to explore these and other possibilities. The holocoenotic principle is undoubtedly operating, requiring a consideration of the interaction of many factors to explain successfully why these plants occur where they do.

Summary

Pressure bomb measurements of diurnal and seasonal plant moisture stress in *Eurotia lanata* and *Atriplex confertifolia* were made during the 1968 and 1969 growing seasons in Curlew Valley, Utah. Highest values were recorded in early to mid afternoons of the driest, hottest periods. Rainfalls of more than eight mm generally resulted in immediate reduction of stress values. Differences in plant distribution patterns could not be explained by differences in plant moisture stress data.

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Effects of Aerial Forest Fertilization with Urea Pellets on Nitrogen Levels in a Mountain Stream

Introduction

Over the past two decades, forest fertilization has progressed from the experimental to a practical management stage. Today, in this country as well as other timber-producing countries, fertilizers are applied to increase forest production. Although phosphorus and other elements have been shown to increase forest production in some parts of the world, nitrogen has most often proved effective in stimulating forest growth (Gessel *et al.*, 1965; Broadfoot, 1966; Klem, 1968). In the Pacific Northwest and western Canada, increased production of Douglas-fir clearly illustrates increased growth response to nitrogen fertilizer (Gessel *et al.*, 1965; Reukema, 1968; Brix and Ebell, 1969).

Recently, large-scale fertilization has been effected through aerial application. During 1969, the authors undertook a limited study in cooperation with Willamette Industries, Inc., Dallas, Oregon, on the effects of aerial forest fertilization on nitrogen levels in a mountain stream. The study considered only the response of the various forms of nitrogen in the stream to the aerial fertilization. Effects of urea pellets introduced directly into the water during the application were taken into account, in addition to washoff and leaching from the adjacent forest land during the next several months.

Methods

The study area was located in Linn County in the western foothills of the Cascade Mountains about 28 miles (45 km) east-southeast of Albany, Oregon. Urea was applied to a 569-acre (230 ha) tract of previously unfertilized forest land, lying at altitudes of approximately 1480 to 2080 ft (451 to 634 m). Forest cover consisted primarily of well-stocked, 35-year-old Douglas-fir. The tract was drained by Crabtree Creek, a small, steep-gradient stream, on which the investigation was conducted. The topography was moderate with steep pitches into the stream beds.

Buckshot size urea pellets¹ were broadcast by helicopter over the study area (Fig. 1) on May 15-19, 1969, at a concentration of 437 lbs/acre (490 kg/ha) which is equal to approximately 200 lbs N/acre (224 kg/ha). Actual periods of fertilization were 1800 to 1930 on the 15th, 0700 to 2000 on the 16th, 0700 to 1800 on the 17th, and

¹ Cominco American Inc., Portland, Oregon forestry grade (46-0-0).

CRABTREE CREEK Study Area

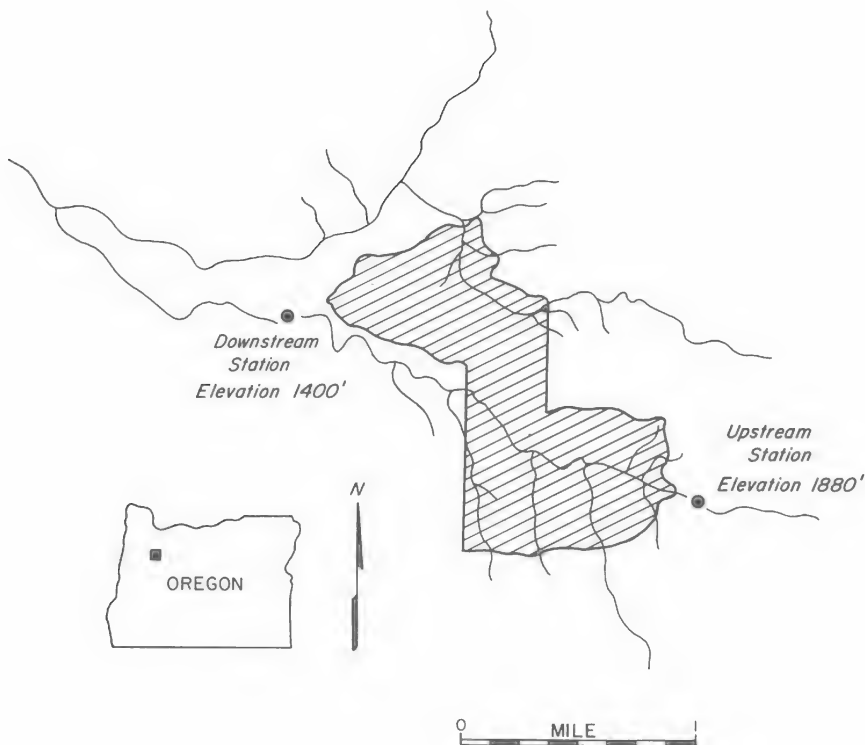


Figure 1. Location of Crabtree Creek study area and sampling stations.

0730 to 1400 on the 19th. The boundaries of the area were marked with colored balloons to provide guidance for the helicopter pilot. Samples were obtained at two monitoring stations, one upstream and one downstream from the fertilized area, on May 6, 7, 9, and 15 to establish the prefertilization chemistry of the stream. Nitrogen levels existing at that time will hereafter be referred to as base-line levels. Fertilizing was initiated on the 15th, but sampling was carried out on that date before the overflights began. Samples were collected approximately every two days for two weeks after fertilization was completed. Intermittent sampling was then continued until January 1970 as a check on further input of fertilizer-nitrogen to the stream as a result of fall-winter rains.

In addition to nitrogen, the primary focus of the investigation, a number of other chemical analyses were made on the samples collected prior to fertilization to provide a chemical characterization of the water. During the monitoring study following aerial fertilization, water samples were analyzed only for ammonia, nitrite, nitrate, and Kjeldahl nitrogen.

At each station, water was collected in one-liter plastic bottles and the samples fixed by addition of four ml of a saturated solution of mercuric chloride. Analyses were performed by Consolidated Laboratory Services of the Pacific Northwest Water Laboratory according to FWQA methods, using the automated Technicon procedures for ammonia, nitrite, and nitrate (U.S. Department of Interior, 1969).

Crabtree Creek was not gaged, and measurements of flow were not obtained. Estimated flow in mid-May was about 10-15 cfs. Maximum streamflow was approximately twice this amount in late fall.

Precipitation data used in this report are those obtained by the Weather Bureau Station at Detroit Dam (U.S. Department of Commerce, 1969), 18 miles (29 km) northeast of the study site.

Results

Urea pellets were analyzed for ammonia, nitrite, nitrate, and Kjeldahl nitrogen. Results were as follows: ammonia-N, 140 mg/kg; nitrite-N, 0.53 mg/kg; nitrate-N, 19.33 mg/kg; and Kjeldahl-N, 440,000 mg/kg. The Kjeldahl nitrogen analysis was chosen to provide an estimate of undecomposed applied fertilizer.

Average prefertilization water chemistry of Crabtree Creek appears in Table 1.

TABLE 1. Average chemical composition of creek prior to fertilization.

pH	7.5
Temperature	10.5°C
Specific conductance at 25°C	21 μmhos/cm
Total carbon	5 mg/l
Total organic carbon	3 mg/l
Sodium	1.2 mg/l
Potassium	0.2 mg/l
Chloride	1.0 mg/l
Soluble silica	9.0 mg/l
Ammonia-N	<0.01 mg/l
Nitrite-N	<0.01 mg/l
Nitrate-N	<0.01 mg/l
Kjeldahl-N	0.4 mg/l
Orthophosphorus	0.004 mg/l
Total phosphorus	0.013 mg/l

Ammonia, nitrite, and nitrate nitrogen were undetectable before fertilization. Kjeldahl-N, however, was present at a concentration of 0.4 mg/l. Except for nitrite, which remained undetectable for the duration of the study, rises occurred in all nitrogen forms following the urea application. Kjeldahl-N increased from 0.2 mg/l on May 15 at the downstream station to more than 24 mg/l on the 16th (Fig. 2). A small concurrent rise from 0.3 mg/l to 1.4 mg/l occurred at the upstream station. The next day values downstream and upstream had fallen to 2.0 mg/l and 0.8 mg/l, respectively; this decline coincided with the cessation of fertilization in that area. By the next sampling date, May 19, Kjeldahl-N had further declined to near prefertilization levels at both stations, although fertilization continued in adjacent areas through the 19th of May. The rise on May 24 at the upstream station to 2.8 mg/l cannot be explained; however, it is the only significant increase of Kjeldahl-N that occurred at either location after May 16.

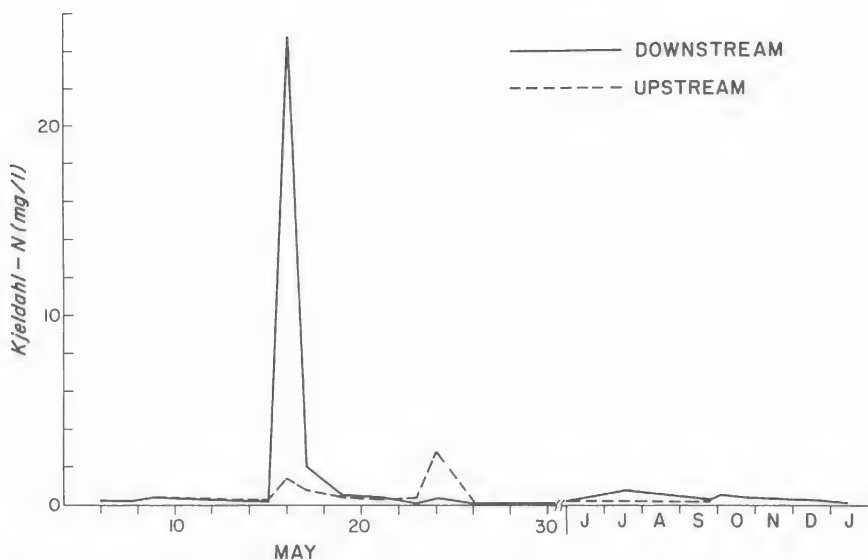


Figure 2. Concentration of Kjeldahl-Nitrogen from May 1969 to January 1970.

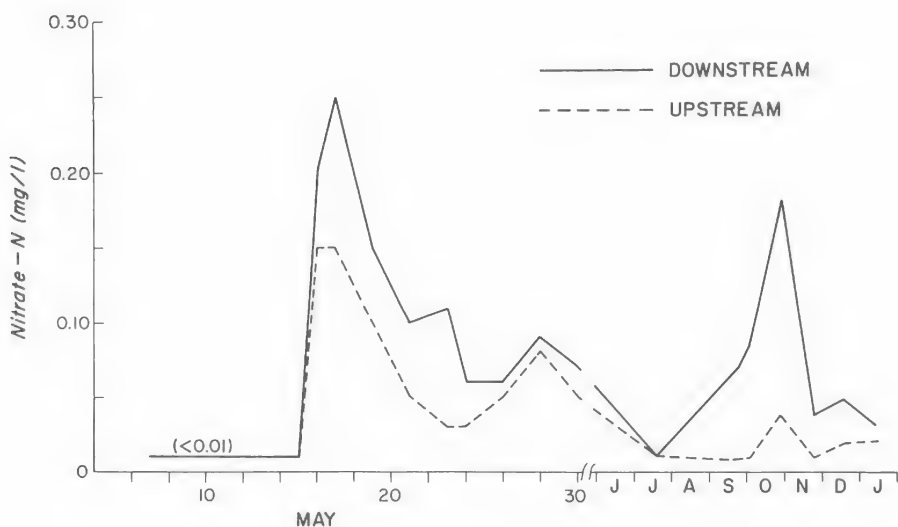


Figure 3. Concentration of Nitrate-Nitrogen from May 1969 to January 1970.

Nitrate-N (Fig. 3) also showed a notable increase from May 15 to 16, from less than 0.01 mg/l at both stations to 0.2 mg/l at the downstream station and 0.15 mg/l upstream. Downstream nitrate-N further increased to 0.25 mg/l on the 17th. Levels then decreased throughout the month of May both upstream and downstream. Samples

collected and analyzed in July indicated that the Kjeldahl and nitrate levels both returned to their prefertilization concentrations.

Precipitation during July and August amounted only to 0.23 inches as measured at Detroit Dam. With an increase in precipitation starting in September, nitrate-N levels again rose above the base line to a maximum of 0.18 mg/l at the downstream station. A slight increase was also noted upstream (Fig. 3). No concurrent rise in Kjeldahl-N was observed; it remained essentially constant throughout the remainder of the study. Sampling was concluded in January when the nitrate-N values appeared to have again returned to near base line.

Results of ammonia determinations have not been graphically represented because of the varying minimum limits of detectability at different times during the study. The data do show the following: base line levels in the stream were <0.01 mg/l ammonia-N. On May 16 values rose to 0.08 mg/l at the downstream station, then fell to at least <0.05 mg/l by the 19th. They continued at or below this level for the rest of the month. Except for a suspect value of 0.24 mg/l on October 3 at the downstream station, ammonia-N fell to prefertilization levels by November and remained there.

Discussion

The significant changes in Kjeldahl-N which coincided with the period of fertilization strongly suggest the effect of direct application to the water. This is in agreement with Cooper (1969) who noted that a major problem of forest fertilization with respect to water quality can be direct application to streams. As indicated by the analysis of the urea pellets, most of the nitrogen in the pellet is detected by the Kjeldahl test; hence, the immediate high values of Kjeldahl-N in the stream seem to indicate the presence of large amounts of dissolved urea resulting from direct application.

The initial increase in nitrate-N also was likely caused by direct application. The maximum observed level of 0.25 mg/l is assumed to have originated in the pellets, which contained over 19 mg/kg of nitrate-N. The extended duration of the elevated nitrate levels suggests temporary retention in the soils and vegetation and a gradual movement to the receiving stream.

The rise in nitrate at the upstream station at the time of fertilization cannot be readily explained. It seems likely that application to that part of the stream occurred accidentally.

The secondary rise in nitrate-N levels which occurred in late summer and fall correlates with precipitation data. Table 2 shows daily rainfall for a two-week period following initiation of the experiment, and monthly totals to January 1970.

Downstream nitrate levels increased through October, sharply decreased in November, and remained at approximately the November level into January. The upstream station reacted similarly but to a much lesser degree. The decrease after October might be attributed to the following: (1) the heavy rains in September and October may have resulted in movement of most of the nonassimilated fertilizer into the stream during that period, or (2) there may have been a more or less continuous supply of nitrate to the receiving stream throughout the fall and into January but the concentrations were reduced as the volume of flow of the stream increased.

It is interesting to compare the results of our work to Cole and Gessel (1965) who reported from their work with lysimeters that 65 percent of the nitrogen from

TABLE 2. Precipitation as recorded at Detroit Dam.

Daily	Inches	Monthly	Inches
May 14	.57		
May 15	.12	June	8.26
May 18	.01	July	0.15
May 19	.72	August	0.08
May 20	.19	September	3.91
May 25	T*	October	7.29
May 26	.25	November	5.06
May 27	.61	December	15.62
May 28	.13	January	24.19
May 29	T*		
May 30	1.18		

* Trace

a urea application to a Douglas-fir forest passed through the top one inch (2.5 cm) of the forest floor during a 30-day period of heavy rains. This same work, however, showed essentially no nitrogen lost beyond the 36-inch (91.4 cm) soil depth.

An attempt was made to correlate daily precipitation records with the May nitrate samples. Although there was a general decline in nitrate during May following fertilization, a temporary rise which occurred at both stations near the end of the month corresponded closely to increased precipitation.

The results of our study appear to agree well with those of McCall (1970), who found that aerial application of fertilizer resulted in rapidly increased urea concentrations in the water, and that this was probably due to direct fallout into the water. He also found that urea levels decreased to background values in a relatively short time and that after a month the nitrogen lost from the land appeared to be in the form of nitrate only.

From the point of view of eutrophication, aerial forest fertilization with urea can be a process by which an important algal nutrient is added to the aquatic ecosystem. As shown in this study, direct application to the water can increase nitrogen levels manifold. Although, as in the case of Crabtree Creek, these elevated values rapidly returned to base line levels, the nitrogen had not disappeared from the water but was simply displaced downstream. Depending on the size and rate of flow of the affected waterway, directly applied nitrogen could be of importance in stimulating unwanted biological production. Therefore, efforts should be made wherever possible to prevent such direct applications.

Our study has further shown that fertilization of the watershed immediately adjacent to the stream results in movement of nitrogen to the water during periods of rainfall. As Cooper (1969) has pointed out, attention must be paid to the riparian zones adjacent to streams, where fertilizers have only a short distance to move to reach the water. He has also noted, however, that fertilization of sites at a distance from streams is less apt to be a problem.

This problem of effect of forest fertilization on adjacent water courses should receive continuing study. Samples should be collected with a greater frequency and composited according to measured stream flow so that an estimate of fertilizer lost to the water course can be calculated. A thorough study of this type would delineate the ground rules for future fertilizer applications.

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Vegetation and Soils of a 30-year Deer and Elk Exclosure in Central Washington

Consumptive uses of forest and associated range plants frequently cause changes in the structure of plant communities. With continuous disturbance these changes generally follow the pattern of simplified vegetative structure and reduced potential for site recovery. In extreme cases the end point is site productivity lowered to that of parent rock.

There is a continuing effort to develop management methods which will minimize erosion associated with general land use and restore hydrologic control on more than two million acres of lands deteriorated from past abuse in eastern Oregon and Washington. Information needed to manage lands for watershed protection, or successfully to rehabilitate deteriorated lands, must be based on understanding of soils, vegetation, and response of both to the influences of alteration by use. One approach is to compare vegetation and soil conditions of areas of use (or abuse) with areas of the same habitat type representing relict or near-relict conditions.

A one-acre deer and elk exclosure established in 1939 near Wenatchee, Washington, provided us the opportunity to study vegetation and soils under conditions of continuous exclusion of game animals in a *Pseudotsuga/calamagrostis* habitat type having *Pseudotsuga menziesii*-*Pinus ponderosa*-*Ceanothus velutinus* and *Calamagrostis rubescens* as dominants. The striking contrast in vegetative aspect between the exclosure and surrounding area drew our attention to this site (Fig. 1). The area inside the exclosure supports a dense stand of snowbrush ceanothus (*Ceanothus velutinus* (Dougl.)) contrasted to a grass- and forb-dominated understory surrounding the exclosure.

Snowbrush ceanothus is known to play a site-ameliorating role in succession through symbiotic N fixation (Delwiche, Zinke, and Johnson, 1965; Wollum, Youngberg, and Chichester, 1968; Wollum and Youngberg, 1964). It invades burned and disturbed areas forming low, dense thickets, thus providing excellent site protection and soil stability (U.S. Department of Agriculture, 1937).

Photos taken five years after establishment support the generally held recollection of long-time residents that snowbrush ceanothus was once as dense outside the exclosure as inside (Fig. 2). Since that time snowbrush ceanothus density outside has declined until there are only a few decadent plants (Fig. 3).

Our objectives in studying this exclosure were to determine the long-term effect of snowbrush ceanothus maintenance on the site and to secure baseline information regarding vegetation and soil characteristics under protected conditions in the ponderosa pine-Douglas-fir zone.



Figure 1. Comparison of vegetative aspect between the enclosure and outside, 1970.

History and Description of the Area

Although the history of use in the Mission Creek drainage is sketchy, it appears that timber in the area was harvested by clearcutting in the early 1930's. Clearcutting and slash burning resulted in the growth of a dense stand of snowbrush ceanothus throughout the area. A report in 1936¹ estimated the winter deer population of Mission Creek at 1200 to 1500 animals. At this time, the need to maintain a balance with the available food supply was stressed. The one-acre enclosure under study was protected with a 12-ft fence by the Civilian Conservation Corps in 1939 as a reference for measuring the degree of grazing use in the Mission Creek area.² Elevation is approximately 3700 ft.

Apparently, efforts at maintaining a balance between big game populations and their food supply were unsuccessful, particularly where snowbrush ceanothus was concerned. This plant is a preferred browse species in north central Washington. A photographic survey in 1944 recorded heavy utilization of snowbrush ceanothus and antelope bitterbrush (*Purshia tridentata* (Pursh) DC.) outside the enclosure (Fig. 4) which was followed by virtual elimination of the snowbrush ceanothus. This was thought to have resulted from a large increase in deer population because of low hunting

¹ Personal communication with Charles F. Banko, District Ranger, U.S. Forest Service, Leavenworth District, Wenatchee National Forest.

² Legal description is S1½ of Section 21, T22N, R19E, Willamette P.M.



Figure 2. View outside the enclosure in 1944. U.S. Forest Service photo.

pressures during World War II. However, this could not be verified by deer route counts because the 1942-1947 period was not evaluated.³

The soil is a sandy loam derived from Swauk sandstone parent material and of the Swauk series. Overstory vegetation consists primarily of ponderosa pine (*Pinus ponderosa* Laws.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). According to Daubenmire and Daubenmire (1968), this site is a *Pseudotsuga menziesii*-*Calamagrostis rubescens* habitat type.

Methods

Since no data on vegetation and soils prior to or subsequent to establishment of the enclosure are available, our approach has been to evaluate characteristics of vegetation and soils of the enclosure relative to an adjacent area where continuing game use has occurred.

Composition and cover of shrubby and herbaceous understory vegetation were measured along six permanent belt transects 43.6 x 2 ft inside and outside the enclosure. Transects were randomly located but were oriented from SW to NE. A one-square-ft wire frame divided into 0.5, 0.25, 0.15, and 0.10-square-ft sections was used to reference crown cover estimates.

³ Personal communication with John Patterson, Washington State Department of Game, Wenatchee, Washington.



Figure 3. View outside the enclosure in 1970 from the same point as Figure 2.

Litter and decomposing plant materials were collected on three random one-square-ft locations on each transect. Soil samples were collected at each of these locations at 0- to 3- and 9- to 12-in depths and analyzed for porosity, pH, organic matter, total N, total S, cation exchange capacity, and exchangeable Ca, Mg, K, Na, and Mn.

Results

Vegetation crown cover between the enclosure and surrounding area showed the greatest difference of any characteristic measured. Total vegetal cover inside the enclosure was 43 percent compared with 21 percent outside (Table 1). Of the individual classes of plants, total shrub cover provided the most striking comparison—cover inside the enclosure was five times greater than outside. Most of this difference was the result of snowbrush *ceanothus* with a cover of 14 percent inside and 0.1 percent outside the enclosure.

Grasses and sedges were dominated by pinegrass (*Calamagrostis rubescens* Buckl.) and elk sedge (*Carex geyeri* Boott) inside and outside the enclosure. Crown cover of grasses and sedges was one-third greater inside the enclosure than outside, with elk sedge accounting for most of the difference.

Western yarrow (*Achillea millefolium* L.), mountain dandelion (*Agoseris* spp.), and Canada hawkweed (*Hieracium canadense* Michx.) were the dominant forbs inside and outside the enclosure. Forb crown cover was slightly higher outside the enclosure, and there was a greater number of species in this location.

The mass of litter and decomposing plant materials was greater inside the enclosure (39,000 lb/acre) than outside (26,100 lb/acre).



Figure 4. Fenceline comparison of area inside the enclosure (left) and outside (right) in 1944. Note heavy utilization of shrubs outside the enclosure.

There were no striking differences between the enclosure and outside for any soil characteristics measured at either depth (Table 2). However, inside the enclosure, there was a tendency for cation exchange capacity to be higher and pH to be lower than outside.

Percent porosity and the concentration of all chemical constituents measured except pH decreased between the 0- to 3-in and 9- to 12-in depths both inside and outside the enclosure.

Discussion and Conclusions

In a comparison of soil properties, it would seem that snowbrush ceanothus had no protracted influence on the site. The uniform total N of the soil between the enclosure and outside was surprising in light of existing information on symbiotic N fixation by snowbrush ceanothus. However, Zavitzkovski and Newton (1968) found that snowbrush ceanothus biomass has a high capacity to accumulate N. The biomass may contain up to 770 kg/ha of N, of which 100 kg/ha is recycled to the soil annually. From this, they estimate that snowbrush ceanothus plants growing in the field may fix up to 20 kg/ha of N annually.

If we consider that total vegetal cover was twice as great inside the enclosure as outside, total biomass must also have been greater—particularly since snowbrush

TABLE 1. Percent foliar cover of vegetation inside and outside the enclosure.

Class of Vegetation	Inside	Outside
Grasses and sedges		
<i>Calamagrostis rubescens</i>	6.59	4.70
<i>Carex geyeri</i>	10.51	5.89
<i>Agropyron spicatum</i>	0.19	0.30
<i>Stipa columbiana</i>	0.13	0.18
<i>Festuca idahoensis</i>	0.11	0.17
Other grasses and sedges	0.17	1.48
Total grasses and sedges	17.70	12.72
Shrubs		
<i>Ceanothus velutinus</i>	14.10	0.12
<i>Purshia tridentata</i>	0.11	1.93
<i>Amelanchier alnifolia</i>	1.39	0.27
<i>Rosa sayi</i>	0.31	0.29
<i>Prunus virginiana</i>	4.64	0.00
<i>P. emarginata</i> var. <i>emarginata</i>	0.29	0.67
<i>Symphoricarpos albus</i>	2.02	0.36
<i>Mahonia repens</i>	0.00	0.64
Total shrubs	22.86	4.28
Forbs		
<i>Achillea millefolium</i>	0.51	1.33
<i>Agoseris</i> spp.	0.46	0.25
<i>Hieracium canadense</i>	0.10	0.68
<i>Lathyrus pauciflorus</i>	0.16	0.25
<i>Potentilla arguta</i>	0.03	0.45
<i>Collinsia</i> spp.	0.03	0.12
<i>Phacelia hastata</i> var. <i>leucophylla</i>	0.61	0.02
Other forbs	0.66	0.80
Total forbs	2.56	3.90
Total vegetal cover	43.12	20.90

TABLE 2. Comparison of some physical and chemical soil properties inside and outside the enclosure.

Property	Inside		Outside	
	0-3 in.	9-12 in.	0-3 in.	9-12 in.
pH	5.95	6.05	6.24	6.35
Porosity	63.93	54.48	64.27	57.89
Organic matter	5.85	2.33	5.61	2.31
Total N	0.19	0.07	0.19	0.08
Total S	0.009	0.004	0.009	0.004
	me/100 g			
Cation exchange capacity	24.42	15.19	21.22	14.79
Exchangeable Ca	11.02	8.06	11.40	8.25
Exchangeable Na	0.16	0.17	0.17	0.18
Exchangeable Mg	1.00	0.74	0.95	0.70
Exchangeable K	1.52	1.14	1.46	1.17
Exchangeable Mn	0.03	0.01	0.02	0.01

ceanothus shrubs comprised most of the difference. Also, the litter layer was one-third greater inside than outside. If the nutrient content of live plant parts, litter, and decomposing plant parts had been accounted for, the total nutrient capital of the enclosure would have been much greater than outside.

Nitrogen fixed by snowbrush ceanothus symbiosis, although not immediately available for growth of other plants, does represent a potentially available reservoir of N for plants which succeed snowbrush ceanothus. Quick (1944) found that Sierra gooseberry grown with nodulated snowbrush ceanothus roots put on twice as much growth as those grown alone. Wollum and Youngberg (1964) concluded that two snowbrush ceanothus plants fixed 35 ppm of N which was available for plant growth after decomposition of the roots. Similarly, Russell and Evans (1966) showed the capacity of snowbrush ceanothus for N fixation to be in the order of 286 mg/plant in an 18-week period.

In light of the results of other workers and our observations on vegetation and litter differences between the enclosure and the outside area, it appears that snowbrush ceanothus does have a significant site-ameliorating capacity.

Vegetation cover, litter accumulation, and soil nutrients were probably at an upper limit in the enclosure because of the complete protection it received.

Without prior information on vegetation and soils, it is impossible to establish vegetative trends of the two areas. Nevertheless, differences in vegetal crown cover and litter accumulation between the enclosure and outside give a clue as to what has occurred since the enclosure was established. If we assume that conditions were uniform across the area in 1939, use has apparently not been intensive enough outside the enclosure to affect soil nutrient levels. Only vegetative composition, vegetal crown cover, and litter accumulation have been affected. Also, crown cover, litter, and soil organic matter appear to be adequate for soil stability outside the enclosure. On the other hand, the area inside the enclosure reached and maintained stable levels of soil nutrients because decomposition of organic and geologic materials and N fixation were just balanced by plant uptake. The result has been a continued increase in biomass and litter within the enclosure.

Nitrogen and S levels in the soil can be related to previous work, but information on proper levels of the other nutrients is sparse and would require extensive study to test their adequacy. Our level of 0.19 percent N in the surface 0-3 in corresponds well with Jenny's (1930) calculated value of 0.15 percent N for a humid forest region with a mean annual temperature of 45°F.

Even though the concentration of N seems adequate for this site, the calculated C:N ratio of 17 for the surface three in of soil indicates that N would be marginally available. According to Black (1968), the critical ratio of C:N lies between 15 and 33.

Our observed level of S of 0.009 percent in the surface 3 in of soil is at the low end of the normal range for soils of 0.01 to 0.06 percent, and the N:S ratio of 21 violates the optimal ratio of 10 (Burns, 1968). This probably results in reduced efficiency of N utilization by higher plants on this site.

Hydrogen ion concentration of the soil in both locations appeared to be high enough for optimum availability of soil nutrients (Black, 1968). The slightly more acidic reaction inside the enclosure was probably a reflection of more litter and decomposing plant parts in that location.

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Evaluating Forest Sites for Potential Growth Response of Trees to Fertilizer¹

Introduction

Greatly intensified forestry practices will be necessary to meet the wood fiber needs of the future. The demand for timber products is projected to increase about 80 percent in less than 30 years (U.S. Forest Service, 1965). A rapid rise in the demand for forest products and a substantial, steady decline in the number of acres of forest land available for commercial timber production have created strong pressures for greatly intensifying forest management practices (U.S. Forest Service, 1969).

A potentially powerful silvicultural tool, forest fertilization, is currently the subject of much interest in connection with meeting needs for substantially increasing growth rate of trees. Evidence is accumulating that fertilizing forest stands has often led to substantially improved tree growth. Fertilizing does not guarantee improvement in tree growth, however. Added nutrients may be fixed in the soil in an unavailable form, volatilized, or lost by leaching. In addition, forest productivity is often more limited by unfavorable moisture and temperature conditions than by nutritional deficiencies.

Costs of applying fertilizer to forest stands in the Douglas-fir region currently average about \$23 per acre. These costs must be regarded as investments in growing stock, and the increased growth must be sufficient to pay back the investment plus interest.

Ecological considerations also are important in making decisions on the use of forest fertilizer. Public awareness and concern over quality of the environment indicate that forest managers will be under constraint to avoid any unnecessary alteration of natural balances. For these reasons, we believe that nutrients should be added only to those ecosystems in which we can be assured of an increase in tree productivity.

We do not now possess the information we need to determine where fertilizer will provide an economic response of tree growth (Strand and Miller, 1969). In this paper, we suggest that any satisfactory model for understanding the environmental interactions that control productivity must include considerations of (1) adequacy of the nutrient supply in soil; (2) adequacy of tree nutrition; and (3) constraints on productivity other than nutrients (such as moisture supply, temperature, and genetic factors). Results of our analyses agree with findings by Gessel, Stoate, and Turnbull (1965) that nitrogen is at present the principal limiting nutrient element

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for growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Therefore, in the following discussion, most of our remarks and illustrations concerning tree nutrition will be limited to nitrogen.

Soil Fertility

Soil fertility is the ability of a soil to supply nutrients to growing plants. A soil is a dynamic reservoir of plant nutrients, the supply of which is regulated by the return of nutrients through litter decomposition, rainfall, biological activity in the soil, and the capacity of the soil to hold nutrients in an available form.

We have long relied largely upon chemical analyses of soil profiles for information on soil fertility although our methods of chemical extraction may be unrepresentative of forest plants (Ralston, 1964; Viro, 1961). Empirical relations have been useful when determined within well-defined soil-classification units. The diversity of soils and climates in the West, however, encourages an approach more closely related to the processes of nutrient uptake and utilization. Even the best methods with radioisotopes (Bowen, 1971) prevent our assessing the total nutrient reserve in heterogeneous soil profiles. The nutrient supplying power of agricultural soils is often measured by bioassay (Jenny *et al.*, 1950). If forest soils are to be studied, however, agricultural bioassay must be altered in two ways. First, forest plants, rather than agricultural crop species, must be used, because requirements for the two kinds of plants are substantially different (Vlams *et al.*, 1959; Waring and Major, 1964). Second, the entire soil profile, or at least the major portion infiltrated with fine roots, must be represented so that concentrations of nutrients, rocks, organic matter, or other parts of the soil system are not modified by mixing.

On the basis of the foregoing requirements for adequately assessing soil fertility, we determined the nutrient supplying power of several soil profiles by growing seedlings of Douglas-fir and Shasta red fir (*Abies magnifica* var. *shastensis* Lemm.) in reconstructed profiles of a number of relatively young, undeveloped forest soils. These growth studies were carried out under a standardized regime which included favorable moisture, temperature, and light.

Soil was collected in the fall for the reconstructed profiles in three- to six-inch layers from the bottom of a two-ft profile upward in a steplike progression. Near the surface, soil material was removed in one- to three-inch layers. After collection, these soil layers were carefully placed into plastic lined, aluminum containers, five inches in diameter and 24 in deep. In initial survey work, four such samples were collected from an area 100 ft square.

After collection, the soil material was allowed to remain in a cool, shaded environment at field capacity for four months. Four pregerminated seeds of Douglas-fir and Shasta red fir were then planted in each soil container. The bioassay was conducted in a growth room with a 21°C, 15-h day; 10°C, 9-h night; and 14-17°C soil temperatures. Light was provided at 1000 ft-c from fluorescent and supplemental incandescent sources. Each soil container was rotated systematically every three days. At weekly intervals, sufficient water was added to bring all soils to their equilibrium weight at field capacity. One hundred samples were thus evaluated at one time. All seedlings were harvested after five months of growth. Plant dry weight produced above the seedling cotyledon was used as an index of soil fertility.

Plant Demand for Nutrients

The nutritional status of a plant reflects the degree to which the soil nutrient supply meets plant requirements under a particular environment. A rapidly growing plant may be under nutritional stress while, on the same soil, another plant with different nutrient requirements or of slower growth habit may be adequately supplied.

A minimum nutrient level is necessary for the formation and development of new foliage and other organs. This nutrient requirement is always met in the case of natural vegetation because, where soil fertility is low, selection has long favored those species with lower requirements. Selected genetic strains show markedly higher requirements for nutrients and the introduction of such genetic stock will increase the need for fertilization (Fritchett and Goddard, 1967; Walker and Hatcher, 1965). Each plant has a level of nutrition that is sufficient to assure optimum growth. Levels above those essential for optimum growth can be attained but do not contribute further to plant growth.

The nutritional level just adequate to maintain optimum plant growth is referred to as the "critical level" (Ulrich, 1952). It is usually assessed by chemical analysis of various parts of a plant particularly sensitive to nutritional stress.

The least nitrogen reported in expanded foliage of Douglas-fir is about 0.6 percent dry weight (Gessel *et al.*, 1960), a value that agrees with those we measured in the foliage of Douglas-fir plants growing under maximum demand in the growth room. Thus, we can assume that living needles with total nitrogen contents of about 0.6 percent have no mobile nitrogen that can be translocated to other tissue.

A critical value for foliar nitrogen has not been firmly established for Douglas-fir, although values as high as 1.7 percent nitrogen may be required (van den Driessche, 1969). Gessel *et al.* (1960) state that all visible symptoms of nitrogen deficiency disappear if foliar nitrogen remains above 1.1 percent during the autumn season.

Unfortunately, the critical level determined in laboratory experiments may be unrealistically high for field conditions. Laboratory experiments are generally conducted with small seedlings grown in water or sand cultures, often under an abnormally demanding environment without the benefit of the normal root-mycorrhizal association. Recent studies in fertilized plantations suggest that less nitrogen may be required under environments representing less than the optimum potential for growth (Tamm, 1968; Sandvik, 1968).

One of the most disturbing practices in assessing foliar nutrition is the usual preference of investigators for sampling during the dormant season (Gessel, 1962; Leyton, 1958; Tamm, 1964). This practice may result in low sampling error, but, by following it, much biological information is sacrificed. Many researchers have found that nitrogen content in foliage varies seasonally (Youngberg, cited by Lavender, 1970; Tamm, 1955; Smith *et al.*, 1970). But only the last authors cited have recommended that the "best time to characterize the differences in nitrogen is during periods of rapid growth after reserves are depleted and demands for nitrogen are large." The period of maximum demand for nutrients varies from place to place and year to year. It can best be characterized by reference to a particular stage in the morphological development of a plant. Thus, the plant's phenology, not a calendar date, determines the time of sampling.

Although it is well documented that new foliage is a sink for nutrients, the source of mobile nutrients in the older foliage has usually been ignored. We submit that this is a basic error. Figure 1 shows the seasonal change in foliar nitrogen of the previous year's foliage in three Douglas-fir trees growing on relatively fertile, clay soil to which sufficient water was provided to secure some second flushing of foliage. The assumed critical level of 1.2 percent foliar nitrogen agrees with that found in similar foliage of plants growing under the most productive environments in the region where our assessment of soil fertility, plant nutrition, and other environmental variables was made (Waring, 1969).

As new foliage expanded, the nitrogen level began to drop and reached a minimum during late summer (Fig. 1). Some recovery took place during the winter although it was not sufficient to restore the nitrogen to its original status. These findings suggest that the most appropriate time to sample tree foliage during the growing season would be after new foliage has fully expanded. We find, however, that maximum nitrogen translocation has already taken place on some sites when the new foliage is only at the "brush stage."

Because the dry weight of needles can vary by more than 20 percent during the growing season, comparisons of nutrient status in plants are difficult unless sampling is confined only to one period. For this reason, expressing concentrations as mg cm^{-3} or some similar units (Tamm, 1955; Tamm, 1964; Cassidy, 1970) would be an additional improvement in assessing seasonal changes in nutrition. We do not favor the practice of reporting results on a per needle or shoot basis; such expressions mainly reflect differences in growth, not nutrition (Tamm, 1964).

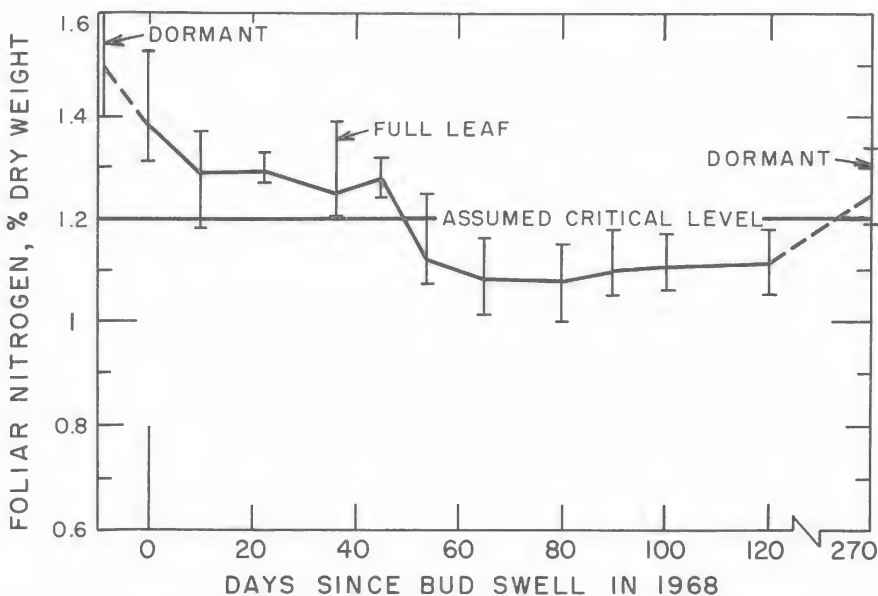


Figure 1. Seasonal variation in nitrogen content of mature Douglas-fir needles (1967 foliage).

Forest Productivity

Plant productivity is a function not only of soil fertility and plant nutrition but also of the genetic potential of a plant and the limitations upon that potential from the entire environment. Drought alone may increase foliar nitrogen to values above 3 percent as Heiner (1968) found in his study of different Douglas-fir populations and Zinke (1962) reported with ponderosa pine growing on poor sites in California. In such instances, adequate fertility and adequate nutrition have little influence upon productivity. This is not an isolated example. Both the vegetative composition and productivity of native forests are more generally limited by moisture and temperature than by inadequate supply of available nutrients (Waring, 1969). Strong winds, snow, and ice may also strictly limit tree growth in many parts of the world by damaging the crown or uprooting exposed trees.

Ecologists have developed various approaches for classifying forest environments. Some of those recently devised are based upon measured environmental gradients (Waring and Major, 1964; Griffin, 1967; Waring, 1971). In the last reference, the productivity and distribution of Douglas-fir and Shasta red fir are depicted as functions of both moisture (Waring and Cleary, 1967) and temperature gradients (Cleary and Waring, 1969). Six of the sampled environments labeled for reference in Figure 2 represent a range of stands dominated by Douglas-fir and Shasta red fir. We can see that Shasta red fir is generally restricted to the cooler environments, usually where moisture stress is not severe. Douglas-fir occupies warmer sites across a complete range of moisture stress conditions. Stand productivity, as indexed by maximum height, decreases with decreasing temperatures and available water.

Interrelations among Soil Fertility, Plant Nutrition, and Productivity

We have distinguished among (1) the nutrient supply in the soil, (2) demand for nutrients by plants, and (3) other constraints on productivity. Now we will focus upon important interrelations to see whether our conceptual model can provide interpretation for a range of real situations.

To do this, we will select some extreme environmental combinations referenced by number in Figure 2. In Table 1, the six ecosystems are referenced again by number, and indices to their soil fertility, foliar nitrogen, and productivity are given. The nutritional data are an average from three trees, 1-2 m tall. Variation among the three trees was rarely more than 0.1 percent nitrogen and less than 0.05 percent in most instances.

Assuming that at least 1.2 percent nitrogen during the active period is necessary to sustain maximum growth for both Shasta red fir and Douglas-fir, then Stand 17 appears nearest to optimum. At that site, soil fertility is high, nutrition is adequate, and productivity is the highest among the listed Shasta red fir stands. Stand 7, on the other hand, appears to have adequate foliar nitrogen only during the dormant season. During the growing season, a decrease to 0.94 percent suggests the limiting ability to supply nitrogen of the soil derived from weathered quartz diorite. Stand 18, also developed on soils derived from quartz diorite, has a limited supply of nutrients in the soil, but more than adequate foliar nutrition during the dormant season. This response could reflect the reduced demand of plants growing near timberline where a lack of soil moisture and the mechanical effect of snow and wind combine to limit productivity. Yet, nutritional stress appears to develop during the growing season.

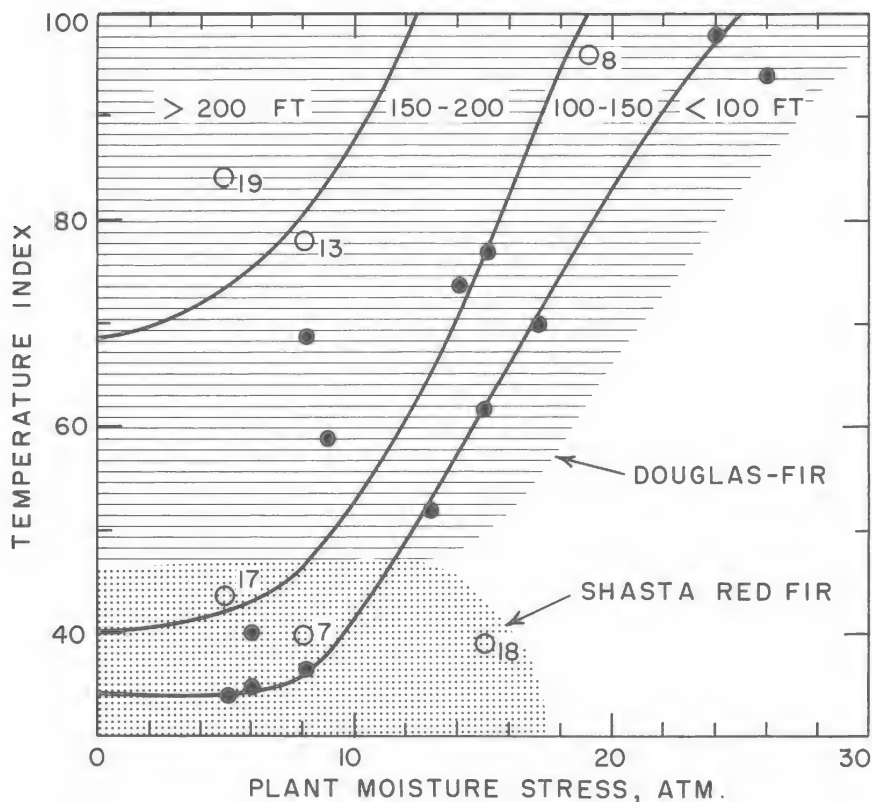


Figure 2. Forest productivity (maximum height) in relation to moisture and temperature. Numbered circles are referred to in text. Moisture stress gradient is based upon the maximum recorded, before dawn, during the growing season in conifers, three to six ft tall. The temperature index represents the potential growth of Douglas-fir, derived by summation of the growth possible each day during the growing season (Waring, 1969).

Ecosystems dominated by Douglas-fir, on soils weathered from quartz diorite, may have temperatures that encourage growth but an inadequate supply of nitrogen even during the dormant season (Stand 8). Moisture stress is a problem in Stand 8, a type dominated by ponderosa pine (Waring, 1969). Here, additions of fertilizer might well increase the nutritional level of the plants without substantially increasing productivity. Stand 13 is located on relatively infertile soils developed from hard green schists. The moisture regime is favorable, and, under such circumstances, the nitrogen level becomes critical during the growing season, but not to the extent that primordial development and foliar expansion are prevented. Increasing the nutritional level through fertilization should increase productivity substantially. The highest recorded productivity in our study of the Eastern Siskiyou Mountains of southwestern Oregon and northwestern California was that of Stand 19. Not only does it have a high index of soil fertility and an excellent moisture and temperature regime, but an adequate nutritional status is maintained throughout the growing season. Because nutritional demands appear

TABLE 1. Soil fertility, nitrogen status, and productivity of Shasta red fir and Douglas-fir in the Siskiyou Mountains of southwestern Oregon.

Stand	Soil fertility		Productivity ³			
	Bioassay,	Coef. of variation	Foliar nitrogen ²		Site index, ft	Maximum height, ft
	% of max. ¹		Dormant, %	Active, %		
Shasta red fir						
17	79	0.42	1.23	1.17	----	158
7	27	.51	1.22	0.94	----	145
18	23	.25	1.46	0.96	----	55
Douglas-fir						
8	28	.13	1.01	0.87	120	----
13	30	.21	1.26	0.82	150	----
19	75	.54	1.34	1.20	190	----

¹ Determined by growing Shasta red fir or Douglas-fir seedlings on reconstructed soil profiled for five months under a standardized environment.

² Determined by micro-Kjeldahl analysis on whole first-year needles sampled from three trees, one to two m tall, in October, 1967, and on the same foliage at the time of "brush stage" the following year.

³ Measured directly on an average of five dominant or codominant trees.

to be met, fertilization is a poor investment. Productivity can probably not be substantially increased, at least through additions of nitrogen alone.

If these interpretations are correct, then forest fertilizer trials should include foliar analyses during both the active and the dormant seasons. Such information compared with *field-defined critical levels* for all of the essential plant nutrients could determine: (1) whether plants really are deficient in something; (2) whether fertilizer is effective in improving the nutritional status, and (3), together with knowledge on moisture stress patterns, whether temperature and other major environmental factors provide a satisfactory model for understanding the environmental interactions that control productivity.

Direct measurement of even the major environmental factors is often impossible, but through a survey of soil and vegetation and with the knowledge of experienced personnel, the major constraints upon productivity can often be estimated adequately. Any attempt to improve productivity through the application of fertilizers should, however, include an assessment of foliar nutrition during both the active and dormant part of the growing season. Increases in the level of nutrition can thus be verified and interpreted in comparison with field-defined critical levels.

Summary

Decreasing forest land area and increasing demands for wood fiber require more intensive forestry. One potential means of increasing production is applying fertilizer. But the questions arise: "Where will fertilizing improve the nutrient status of trees and will such improvement lead to increased growth?" To answer these questions, we must assess how nutrients in soil become available to plants and thus increase their growth. To do this, we must distinguish among (1) the nutrient supply in the soil, (2) demand for nutrients by plants, and (3) other constraints on productivity.

In evaluating the nutrient supply in soil, we reconstructed soil profiles and grew

tree seedlings in them under a demanding, standardized environment. We determined plant demand for soil nutrients in the field, assessing the level of foliar nitrogen in the previous year's needles during the period of peak demand when new foliage was expanding and during the previous dormant season.

From an environmental classification, we were able to recognize when other constraints such as moisture and temperature would make forest fertilization an unlikely economic venture and possibly an ecological mistake. The treatment of these problems was not definitive, but with some modifications, the approaches suggested should have wide application.

Acknowledgments

Many valuable ideas come through informal exchanges. Waring, during his recent sabbatical, had an opportunity to discuss many of the points raised in this paper with European scientists. Where a particular idea originated is often difficult to establish, but many of the points raised in this paper were discussed at length with Werner Koch, University of Munich, L. Leyton, Oxford University, and C. O. Tamm, University of Stockholm, and to these men formal acknowledgment is given. In addition, we are particularly indebted to Robert Tarrant, of the U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Corvallis, for critically reviewing the manuscript. This work was supported through a McIntire-Stennis Federal Grant.

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Association News

The 45th annual meeting of the Northwest Scientific Association will be held on the campus of Western Washington State College, Bellingham, Washington on March 23-25 (from noon Thursday to noon Saturday).

In addition to the Association's regular technical sessions, the meeting will feature a timely symposium on "Research on Coniferous Forest Ecosystems: First-Year Progress in the Coniferous Forest Biome, US/IBP." The symposium organizers (Jerry Franklin of the U.S. Forest Service, Dale Cole of the University of Washington, and Richard Waring of Oregon State University) have prepared an outstanding program that will have interest and value for *all persons concerned with ecosystem analysis*. About thirty invited papers will be given during the 1½-day period of presentations.

Also worthy of note, the traditional formal banquet has been replaced with an *informal* Friday evening spaghetti dinner, including appropriate beverages. Plan now to come—and bring your families.

Information about on-campus housing and local hotels and motels will be mailed with the program for the meeting early in March. For further information or any help you may need, write or call one of the co-chairmen for program and arrangements—Willard A. Brown or W. Louis Barrett, Physics Dept., WWSC, telephone 206-676-3819.

* * * *

Copies of "The Biology of Alder," proceedings of a symposium at the 1967 annual meeting, are still available in quantity or singly; free on request to the Director, Pacific Northwest Forest & Range Experiment Station, Box 3141, Portland, Oregon 97208.



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Correlation of West Blacktail Ash with Pyroclastic Layer T from the 1800 A.D. Eruption of Mount St. Helens¹

We recently described a thin, intermittent, but pedologically distinctive volcanic ash layer, the West Blacktail ash, that occurs in northern Idaho as well as in adjacent Washington and Montana (Smith *et al.*, 1968). Later, while considering pyroclastic layers as general contributors to soils in the Pacific Northwest, we observed the mineralogical similarity between this ash and young ejecta from Mount St. Helens, called the lapilli deposit of 1800 A.D. by Lawrence (1954), but renamed layer T by Mullineaux (1964). In this paper we report (1) the occurrence of layer T in the Cascade Range in Washington, beyond the fallout area recognized during the field conference of INQUA in the Pacific Northwest (Schultz and Smith, 1965); (2) our current information on the distribution of West Blacktail ash; (3) some bases for correlating layer T and West Blacktail ash; and (4) relationships between these pyroclastic layers and soil horizonation.

Pyroclastic Layers from Mount St. Helens

Mount St. Helens is a Recent volcano in southwestern Washington, in the Cascade Range. Ejecta include three silica-rich pumice layers, currently named Y, W, and T (Crandell *et al.*, 1962; Mullineaux, 1964). Verhoogen (1937) mentioned the occurrence of pumice north and east of the volcano, and may have examined each of the three layers, although he was primarily concerned with other aspects. Lawrence (1938, 1939, 1954) examined pyroclastic deposits near Mount St. Helens, in connection with his botanical research. He was primarily interested in the pumice that damaged but did not kill Douglas-fir trees south of Spirit Lake, *ca.* 8 km northeast of the volcano. By measuring growth rings he established 1800 ± 2 A.D. as the eruption date. Mullineaux (1964) recognized the probable equivalence of Lawrence's lapilli deposit and his own layer T. We have read Lawrence's field notes, and also have examined and identified pyroclastic samples that he collected; we agree that he was studying material

¹ Scientific Paper No. 3749. College of Agriculture, Washington State University, Pullman, WA. 99163, Project 1869.

that would now be called layer T. He distinguished it not only from a deposit that would now be called layer W, but also from a post-T ash.² He called the latter 1842 ash, and presumed Mount St. Helens to be the source.

Carithers (1946) had available both Verhoogen's paper and Lawrence's initial reports. We infer that he examined the three layers, subsequently named Y, W, and T, as well as interbedded sediments and probably a post-T ash. He equated his younger pumice with Lawrence's lapilli deposit (layer T). When Mullineaux and Meier (*in* Schultz and Smith, 1965) considered the entire Mount St. Helens region investigated by Carithers, extending northward to the Cowlitz River vicinity, they concluded that his younger pumice was chiefly layer W but included layer T in places, and that his older pumice was layer Y.

Most of the current information³ that is directly applicable to this paper is summarized in parts of INQUA Guidebook J (Schultz and Smith, 1965). Pumice in layer Y contains no ferromagnesian minerals other than hornblende and cummingtonite. Its source is an eruption 3000 to 3500 radiocarbon years B.P. Pumice in both the W and T layers contains plagioclase, hornblende, magnetite, and hypersthene, but only the T pumice contains augite. Also, hypersthene from W has higher refractive indices. The eruption which produced layer W occurred 400 to 500 radiocarbon years B.P., whereas that which produced layer T occurred in 1800 ± 2 A.D.

Layer T in the Cascade Range⁴

For orientation, we collected samples within the area of distribution of layer T as reported in Guidebook J (Schultz and Smith, 1965). Both the stratigraphy at the sites and the mineralogy of samples conformed with descriptions by Mullineaux (1964), Mullineaux and Meier (*in* Schultz and Smith, 1965), and Wilcox (1965).

The common presence of layer T within 50 km northeast of Mount St. Helens, as well as our identification of layer T as the parent material of soil horizons sampled at distances of 80 and 95 km northeast of the volcano, prompted several days of reconnaissance at distances of 50 to 100 km from the volcano. This is beyond the geographic limit for T reported in Guidebook J. Although soil profiles (Spodosols) with an A2 horizon developed entirely from layer W were common, we did locate 12 sites

² Our field experience with this post-T ash is principally in the Spirit Lake-Timberline vicinity, where it is usually in contact with layer T, and some mixing is normal. Identifying properties are position in the profile, high silt content, and a 5YR to 7.5YR hue of variable but intermediate value and low chroma. One sample was collected over partly decayed wood. Since there were no incorporated fragments of T pumice, we believe that this 2- to 3-cm layer of post-T ash remained pure after fallout, and was covered by developing O1 and O2 horizons. The sample consisted of fragments of gray and weak red andesite, as well as fragments of very dark gray and weak red scoria, with silt > very fine sand > fine sand > medium sand = coarse sand > very coarse sand. These size separates have the limits established by the U.S. Department of Agriculture (Soil Survey Staff, 1951): silt, .05-.002 mm; very fine sand, .1-.05 mm; fine sand, .25-.1 mm; medium sand, .5-.25 mm; coarse sand, 1.0-.5 mm; and very coarse sand, 2.0-1.0 mm.

³ Mineralogical, stratigraphic, and chemical studies of pyroclastic layers from Mount St. Helens are in reports by Crandell *et al.* (1962); Hopson *et al.* (1962); Mullineaux (1964); Czamanske and Porter (1965); Wilcox (1965; *in* Nasmith, Mathews, and Rouse, 1967); Crandell and Mullineaux (1967); Crandell (1969a, 1969b); Westgate, Smith, and Nichols (1969); Norgren, Borchardt, and Harward (1970); Westgate, Smith, and Tomlinson (1970); Borchardt, Harward, and Schmitt (1971); Randle, Goles, and Kittleman (1971).

⁴ Site locations are available from the writers. Samples were cleaned prior to their study. Organic matter was removed with 30 percent hydrogen peroxide, and iron oxide with sodium dithionite-citrate (Aguilera and Jackson, 1953). Clastic samples were size-separated with sieves. Separates were examined under wide-field and polarizing microscopes. Refractive index was determined by observing the Becke line, using Cargille index of refraction liquids.

with A21 and IIA22b horizons developed from discrete layers of T and W, respectively; one site had a single A2 horizon developed from layer T only slightly diluted by layer W, overlying a lithic IIBirb horizon. Most of these sites lie within a narrow band, but this is true only because the available time limited the extent of our search for the lateral spread of fallout of layer T to a few roads. Within 100 km of Mount St. Helens, then, we identified layer T in soil horizons sampled at 22 sites, and 13 of these were beyond the 50-km arc (Fig. 1).

Samples collected between the 50- and 100-km arcs contained enough pyroclastic fragments larger than 1 mm in both layers (T and W) to permit comparison with fragments of similar size collected less than 50 km from the volcano. In layer T there are usually a few fragments with augite crystals still embedded in the volcanic glass; these rod forms of augite are not present in layer W.⁵ Phenocrysts of hypersthene are found in both the T and W layers, but the hypersthene from T has lower refractive indices. Also, rod forms of hypersthene are dominant in T, but prism forms are more abundant in W. The refractive index of most glass shards is between 1.498 and 1.500 for T, but it is near 1.495 for W. An additional useful property is the much higher concentration of mafic phenocrysts less than 0.1 mm in size embedded in fragments of the dacitic glass in layer T.

Although layer T is less than 1 cm thick at Granite Lake, it is coarser than W, which is 2 to 5 cm thick at that site. A report of layer W as far as 190 km north-northeast of the volcano (Mullineaux and Meier, *in* Schultz and Smith, 1965) was the basis for extending the search for sites with sequential layers of T and W into the area beyond the 100-km arc (Fig. 1). But, since we did not find such sites between Granite Lake and the Yakima River, we sampled the single pyroclastic layer observed in an A2 position in many soils, and tested it for the presence of both T and W. The very coarse sand separate, which is sparse at Granite Lake, first became rare and then was absent from samples collected along this northeasterly traverse. Consequently, the distinction between T and W based on the concentration of small mafic phenocrysts in glass fragments larger than 1 mm was not helpful when we had to rely on inspection of crystal ash of coarse and medium sand size. However, if T and W were the only reasonable possibilities, T in the mixture could still be recognized by the presence of euhedral rod forms of augite with attached volcanic glass, and of euhedral rod forms of hypersthene with a refractive index (n_α) of <1.700 ; W could be recognized by the absence of rod forms of augite, and by the presence of both rod and prism forms of hypersthene with a refractive index (n_α) of >1.700 . Using these criteria, we found a decreasing contribution of T in the single pyroclastic layer as we approached the 150-km arc. Nonetheless, among the samples collected between the 100- and 150-km arcs we identified six as layer T.

The next area for study, beyond the Yakima River, between the 150- and 200-km arcs, was suggested by an extension of a band drawn through the sites already mentioned (Fig. 1). This choice was also supported by a single sample of layer T collected northeast of Cle Elum on Teanaway Ridge, 165 km from Mount St. Helens. Although near-surface pyroclastic layers were fairly easy to find on and near Teanaway Ridge,

⁵In the lower part of the post-W pyroclastic sediment, and the upper part of layer W, we often observed a little andesitic ash with prism forms of augite. Other ferromagnesian minerals are prism and rod forms of hypersthene, $n_\alpha \leq 1.688$, and brown hornblende. The volcanic glass is andesitic, $n = 1.525$ -1.530.

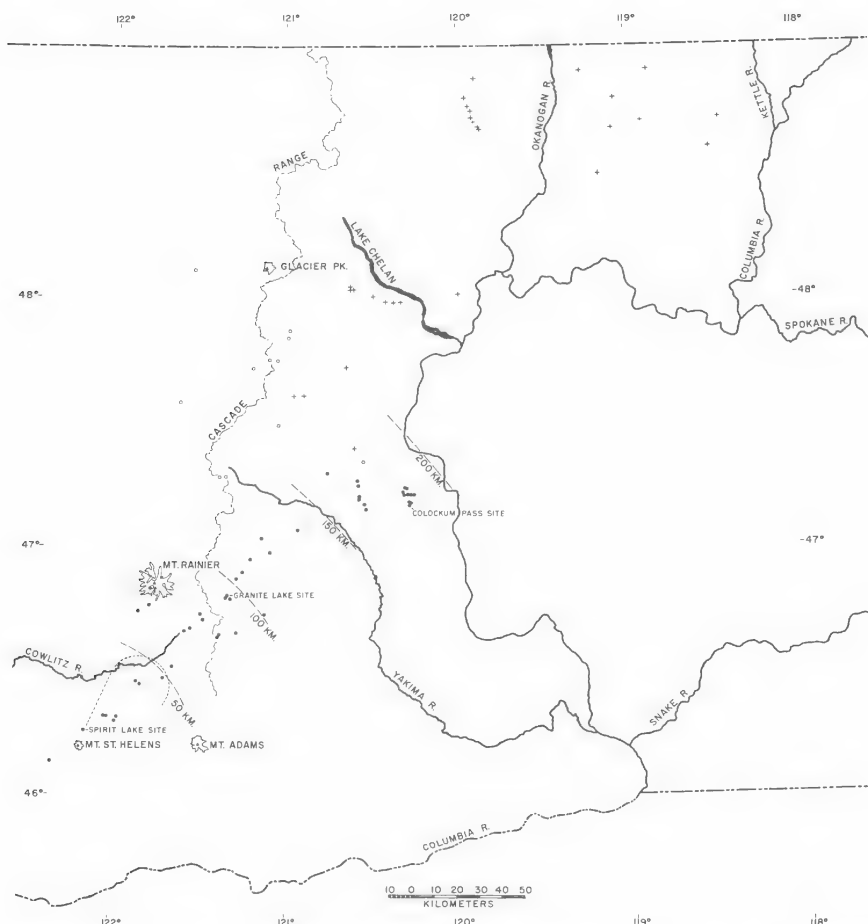


Figure 1. Site locations for samples of Mount St. Helens pyroclastic layer T (symbol •) collected in southwestern Washington. The distribution of layer T known in 1965 (Schultz and Smith) was within the curved dashed lines starting near the Spirit Lake site, and extending northeastward about 50 km from the volcano. Between Mount St. Helens and the Yakima River most of our sampling was within a narrow band; hence, the fallout area is undoubtedly wider than that implied by site locations. Three other pyroclastic layers in A2 positions were encountered and sampled that could be confused with layer T unless their mineralogy was determined. One is Mount St. Helens layer Y (symbol o) in the northern part of the Cascade Range in Washington. Another is a layer (symbol +) south of Lake Chelan and in the Okanogan Highlands that is mineralogically similar to Glacier Peak pumice, although we did not trace it to that source. A third is Mount St. Helens layer W where layer T is absent or minimal, commonly observed in areas northeast of the volcano; sites are omitted from this map.

other samples collected there (T2IN-R16 and 17EWM) had properties of layer W, rather than of layer T.

We next found layer T on Jumpoff Ridge, southeast of Wenatchee, where it is about 1 cm thick, commonly over a thin lithic IIBirb horizon, in soils above about 1525 m (5000 ft) elevation, *i.e.*, above *Pinus ponderosa* forests. This find led to sampling

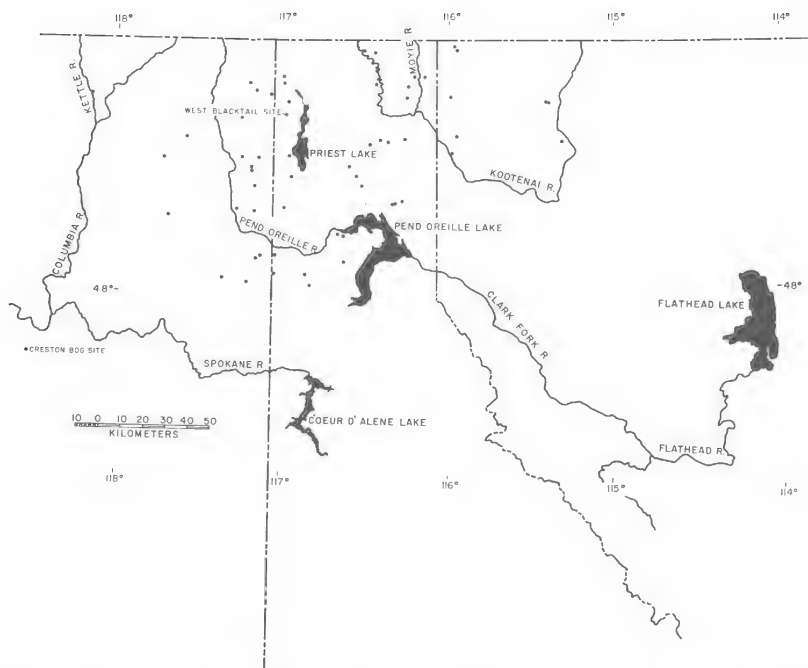


Figure 2. Site locations for samples of West Blacktail ash collected in northeastern Washington, northern Idaho, and northwestern Montana. Another pyroclastic layer that could be confused with West Blacktail ash, unless its mineralogy is determined, occurs at the soil surface north of the West Blacktail sites and just beneath the West Blacktail ash at many of the northern sites shown in this figure. Samples of this layer were collected on both sides of the 49th parallel between 114° and 121° longitude. The volcanic source was not determined; sites are omitted from this map.

of sites shown as a cluster of 10 dots near the 200-km arc, 10 to 15 km west of the Columbia River (Fig. 1). Four of these sites are on Jumpoff Ridge, two are on Naneum Ridge, and four are along the Colockum Pass road (all are in T20N-R20EWM). Here layer T is nearly continuous wherever there is moderate protection by forest litter. We found no trace of layer W either at the plotted sites or during examination of adjacent soils.

The extensive presence of layer T 10 to 15 km west of the Columbia River, between the 150- and 200-km arcs, led to a search of Table Mountain, north of Ellensburg. Although layer T is thinner and less consistently retained there than was observed farther east, it is still easy to find and to sample. A half day of searching produced the string of six closely spaced sites in Figure 1, west of the Colockum Pass site. These are along the Table Mountain road (T19, 20, and 21N-R18EWM). North of Lion Rock pyroclastic layers were difficult to find and those observed were intermittent and often covered by disturbed IIBir horizons. In the field they were presumed to be layer W, which was not found during reconnaissance south of Lion Rock, and this identification was confirmed in the laboratory. Although we recognized no profile with layer T over layer W during the first trip, we did identify both in one monolith

when it was examined in the laboratory. When the site was reexamined during a later trip the presence of both layers was confirmed. The profile has an intermittent 1- to 2-mm layer of T within the O2 horizon, above layer W, which forms the IIA22b horizon. The site (NE $\frac{1}{4}$ NE $\frac{1}{4}$ 33-T21N-R18EWM) is shown by the northernmost dot of the string of six plotted between the 150- and 200-km arcs in Figure 1. It is 170 km from Mount St. Helens.

Between the 150- and 200-km arcs, then, the most easterly sample of layer T is 185 km from Mount St. Helens. It is representative of an extensively observed pyroclastic layer, about 1 cm thick, collected on Jumpoff Ridge, Naneum Ridge, and Table Mountain, and along the Colockum Pass road. Retention along the eastern margin of the area is limited to forests above the *Pinus ponderosa* zone, where it was protected by well-developed O1 and O2 horizons. However, this pyroclastic material must have fallen farther east, beyond the Columbia River, in the semiarid part of central Washington.

West Blacktail Ash

We have already presented some details about the West Blacktail ash (Smith *et al.*, 1968). We considered it a single depositional unit because of (1) its surface position and very abrupt lower boundary in many soils over a large area; (2) its uniformly high proportion of vesicular forms among the glass shards; and (3) the consistent presence of certain glass-encased phenocrysts (particularly hypersthene) of distinctive morphology. We postulated a storm-induced fallout of volcanic ash from an unspecified source, while the air mass and its suspended pyroclastic dust were moving across northeastern Washington, northern Idaho, and northwestern Montana, along a northwest to southeast path. Support for this view included the regular patterns of increasing glass as a fraction of volcanic ash (from .08 to .71) and decreasing hypersthene as a fraction of glassy phenocrysts (from .35 to .06), in the very fine sand separate of 21 samples collected along northwest to southeast lines in northeastern Washington and northern Idaho (Smith *et al.*, 1968). After considering the age of the underlying wood,⁶ an 1853 account of a prominent surface ash layer observed in the area, and Indian legends of ash fallout, we concluded that the ash was older than 1853 A.D. but younger than 250 B.P.⁷

Subsequent to submitting the 1968 manuscript we examined additional soil profiles within the known area of occurrence of West Blacktail ash, searched for the margins of the fallout area, and examined samples collected at new sites. Our current information about distribution of this layer is in Figure 2, with the location shown for 21 old and 36 new sites where we have confirmed the presence of West Blacktail ash. The new data (not shown) for glass as a fraction of the volcanic ash and hypersthene as a fraction of glassy phenocrysts, both in the very fine sand separate, fit well into the patterns already published (Smith *et al.*, 1968). For example, these numbers for the Creston Bog site, southwest of the confluence of the Columbia and Spokane

⁶The WSU Radiocarbon Dating Laboratory reported < 250 B.P. for the age of four samples (WSU Nos. 675, 676, 677, and 905).

⁷In our first paper (Smith *et al.*, 1968) we accepted 1770 A.D. as a reasonable estimate of the date of the ash fall (Teit, 1930). However, Ray (1932) comments that "There is considerable disagreement among natives as to the date of this event. Reckoning is in terms of the approximate ages of various ancestors at the time of the occurrence. Teit's informant placed the date at 1770, but all of my informants agreed that it was after the turn of the century."

ivers, are .31/.36, and for the most easterly sample, within the bend of the Kootenai River in Montana, are .78/.05.

We believe that an area encompassing the site locations in Figure 2 is reasonably close to the area of significant fallout and retention of West Blacktail ash. We have searched beyond the periphery of this area, except for the eastern margin along the Kootenai River, without being able to find West Blacktail ash, even though the sites were promising, *i.e.*, approximately level, with old trees and thick litter, or preserved rotted logs to protect the ash.

Correlation of Mount St. Helens Layer T and West Blacktail Ash

We have chosen only four sites to illustrate the relation between these two pyroclastic materials, although supporting data were obtained for other sites shown in Figures 1 and 2. One sample of layer T is from Granite Lake, 95 km from Mount St. Helens; identification is based on mineralogy, the presence of layer W underlying layer T, and particle size distribution in relation to samples collected closer to the volcano. The second sample of layer T is from Colockum Pass, 185 km from Mount St. Helens; identification is based on mineralogy, particle size distribution in relation to samples between Granite Lake and Colockum Pass, and the presence of the same layer T as well as an underlying layer W at a site 25 km toward the northwest. The third sample is from the western uncultivated end of Creston Bog, 330 km from Mount St. Helens; it occurs as an intermittent layer a few mm thick, usually disturbed by roots, at a depth of about 10 cm; identification is based on mineralogy, particle size distribution in relation to samples from Colockum Pass and the West Blacktail clearcut area, and position in the profile. The fourth sample is representative of West Blacktail ash at the West Blacktail clearcut area, 480 km from Mount St. Helens; thickness of the layer and near-maximum content of diagnostic phenocrysts result in easy sampling and positive identification.

These four samples have the same suite of glass-encased phenocrysts (Table 1), which includes euhedral rod forms of augite, and rod forms of hypersthene with a refractive index (n_{α}) of <1.700 . In each layer the glass shards have a refractive index between 1.497 and 1.501; in the finer sand separates of each layer the glass is dominantly coarse vesicular. At Granite Lake, layer T consists chiefly of coarse and medium sand particles; at Colockum Pass the ash is chiefly fine and medium sand; at Creston Bog and West Blacktail the ash is dominantly silt, but the sand is coarser at Creston Bog (Table 2). These textural differences are in agreement with a postulated single source. The correlation of these two layers, then, is supported by their age, their mineralogy, and their particle size distribution.

There is a gap of 160 km between the most northeasterly sample identified as Mount St. Helens layer T (Colockum Pass road) and the most southwesterly sample identified as West Blacktail ash (Creston Bog). Possible explanations include: (1) the layers are not genetically related; (2) there was continuous fallout across this gap, but only intermittent retention as a discrete layer, because of the lack of suitable cover; and (3) the layers have a single source, but chiefly sand-sized fragments constituted a continuous fallout from Mount St. Helens toward the northeast, whereas the silt and clay particles were carried by an upper air mass until there was a storm-induced fallout starting in northeastern Washington.

The first hypothesis cannot be ruled out, since not all pyroclastic materials in the

TABLE 1. Components of pyroclastic layers.¹

Separates mm	Glass and feldspar	Hypersthene	Hornblende	Augite	Magnetite	Accessory ejecta
Granite Lake Site, 95 km from Mount St. Helens						
>1.0		S . . .	Fragments of pumice	R . . .		NF
1.0 -.5	D	S	S	R	NF	C-S
.5 -.25	D	C	C	S-C	NF	C
.25-.10	A	C	C	S	R	C-A
.10-.05	A-C	S	C-S	R	S	D-A
Colockum Pass Site, 185 km from Mount St. Helens						
1.0 -.5	D	NF	NF	NF	NF	S
.5 -.25	D	C-S	S	R	R	C-S
.25-.10	A	A	C	S	R	C-S
.10-.05	A	C	C-S	S	C-S	A
Creston Bog Site, 330 km from Mount St. Helens						
.5 -.25	D	NF	NF	NF	NF	S-R
.25-.10	D	C	C	R	S	S
.10-.05	D	A	C	R	C	C-S
West Blacktail Clearcut Site, 480 km from Mount St. Helens						
.25-.10	D	C	S	NF	S	S
.10-.05	D	C	S	R	S	S

¹ D (dominant) > 50 percent; A (abundant) 50-20 percent; C (common) 20-5 percent; S (sparse) < 5 percent; R (rare) absent from some samples; NF (not found).

TABLE 2. Particle size distribution of pyroclastic layers.

Layer	Separate (mm) as % of mineral soil					
	VCS 2-1	CS 1-.5	MS .5-.25	FS .25-.1	VFS .1-.05	Silt + Clay ¹ < .05
Mount St. Helens T						
Granite Lake Site	6	54	30	2	1	7
Colockum Pass Site	< 1	2	13	66	2	17
West Blacktail ash						
Creston Bog Site	0	0	1	27	10	62
West Blacktail Clearcut Site	0	0	0	5	22	73

¹ This combined separate is dominantly silt (.05-.002) in each sample. We do not report the percentages individually because of extremely variable breakdown of the silt-sized volcanic glass during dispersion of replicate samples.

Pacific Northwest have been described and identified at their source. However, of the several known sources for silica-rich ash falls in the Pacific Northwest (Wilcox, 1965), only Mount St. Helens has a dated important eruption within the time limits established for the West Blacktail ash: older than 1852 A.D. but younger than 2500 B.P.⁸ This eruption, with an accepted date of 1800 ± 2 A.D., produced layer T.

We have not tested the second hypothesis except for searching a few ponded areas on one reconnaissance trip. However, the presence of about 1 cm of layer T as close as 10 to 15 km west of the Columbia River, where forest conditions resulted in its preservation, makes fallout east of the river a near certainty, in semiarid central Washington.

⁸ Other pyroclastic layers may be added as detailed studies in the Cascade Range are completed. For information concerning known minor eruptions within these time limits, see Mullineaux, Sigafoos, and Hendricks (1969) and papers cited by them.

This paper provides some support for the third hypothesis, or a combination of the second and third. Further searching for pyroclastic layers preserved near the surface of ponded areas between Colockum Pass and Creston Bog may be warranted.

Layer T and Soil Morphology in the Cascade Range and Adjacent Areas

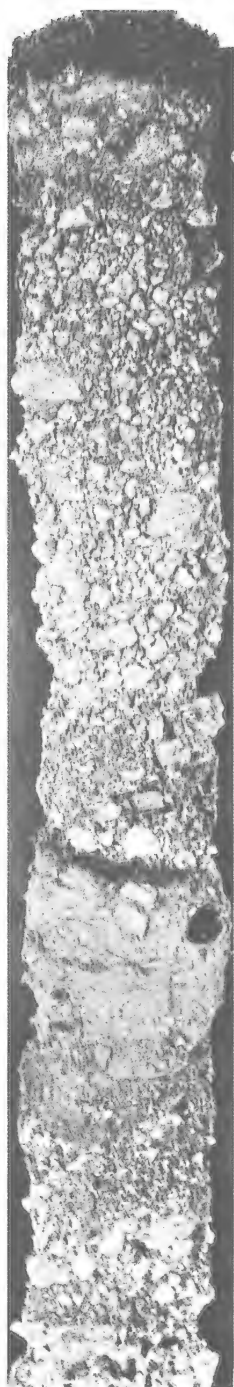
Considering climate and vegetation in the Cascade Range, one would anticipate Spodosol tendencies, and the National Atlas soil map (Soil Conservation Service, 1967) does show the presence of Orthods. But, differing inherent colors of layers and their variable susceptibility to *in situ* weathering often make it difficult to name soil horizons in the field.

In the Timberline-Spirit Lake vicinity surficial organic horizons are usually well formed and easily interpreted, but O2b horizons are often intruded by roots, which can cloud horizon recognition. Fragments of T pumice within or just under O1-O2 horizons, or those mixed with the post-T ash, are often sufficiently lighter in color than underlying pieces to suggest cheluviation. Their 10YR hue contrasts with the 7.5YR hue for very thin illuvial (?) coatings on surfaces and along fractures of underlying T fragments. We infer maximum cheluviation under thick decaying wood, since T pumice there is commonly white (10YR 8/1, dry) instead of the more usual grayish brown or light gray (10YR 6-7/2-2.5, dry) in the IIA22 horizon. Possible buried A2 horizons develop within sediments between layers T and W, and at the top of W. Horizon differentiation is best supported in materials I and II: post-T ash and layer T (Fig. 3-A).

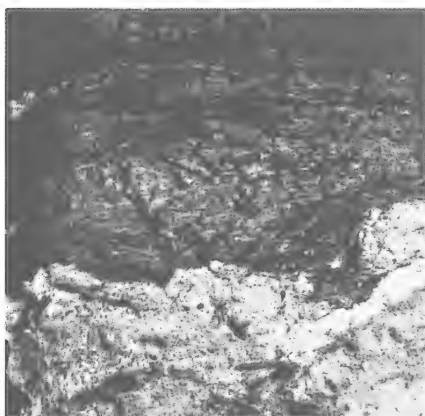
Northeast of Spirit Lake, but still within a distance of 50 km from Mount St. Helens, layer T is several dm thick; colors support an A2-Bir sequence developed from that layer. Farther from the source, where layer T thins to about 1 dm, all or most of it is an A2 horizon. But, since it is difficult to distinguish between the effects of illuviation and gleization within post-W sediments, and of illuviation *vs* weathering *in situ* within layer W, horizon symbols beneath layer T are poorly supported.

Beyond the 50-km arc, in the White Pass-Bumping Lake area, striking profiles result from horizon differentiation of several layers (Fig. 3-B). Cheluviation has consistently produced a light gray to white (10YR 6.5-8/1, dry) A21 from layer T, and a gray (10YR 5-6/1, dry) IIA22b from post-W sediment. Where O horizons are exceptionally thick, or are dominated by decaying wood, layer W becomes a uniformly gray or light gray (10YR 6-7/1, dry) IIIA23b horizon. But under normal O horizons layer W produces a IIIA23b-IIIB21rb combination that is gray with brown mottles of 10YR or 7.5YR hue, and a full range of contrast, abundance, and size. In areas where the sequence of materials is incomplete, and buried profiles are not evident, the horizons are O-A2-IIBir. The A2 has formed from W with admixtures, or more rarely from a locally thickened layer T with W absent. In these profiles material II is variable but often not pyroclastic.

Many profiles sampled northeast of Bumping Lake, between the 100- and 150-km arcs, have O-A2-IIBir horizons. Most A2 horizons have developed from layer W but a few have formed in mixed T and W, or even T alone. Development of color in the Bir horizons is moderate. No profile was found in this area with a clear sequence of all anticipated pyroclastic layers, but our search was limited to promising sites near forest roads.

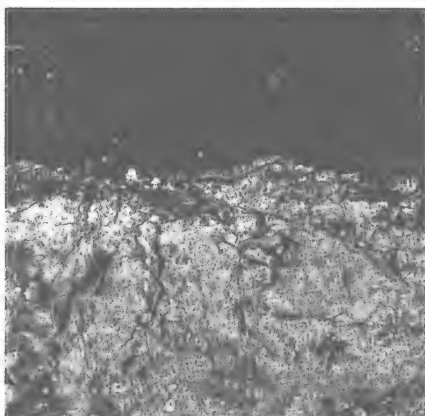


A



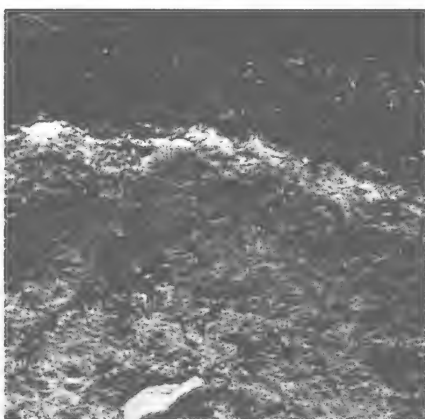
B

GRANITE LAKE



C

COLOCKUM PASS

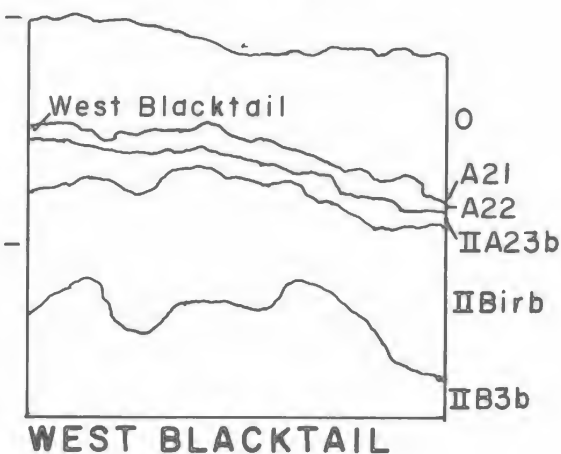
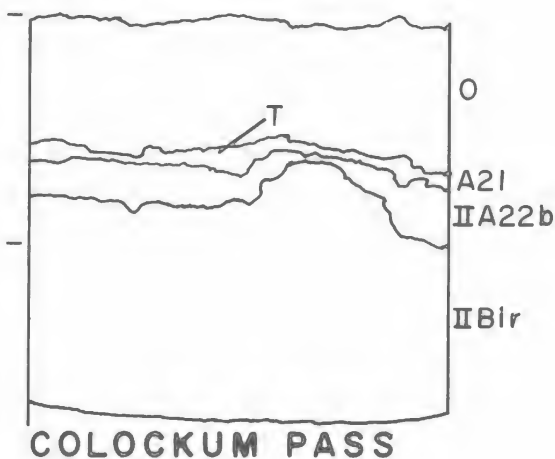
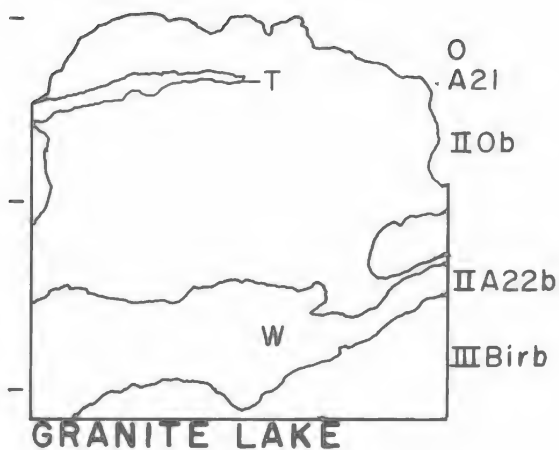
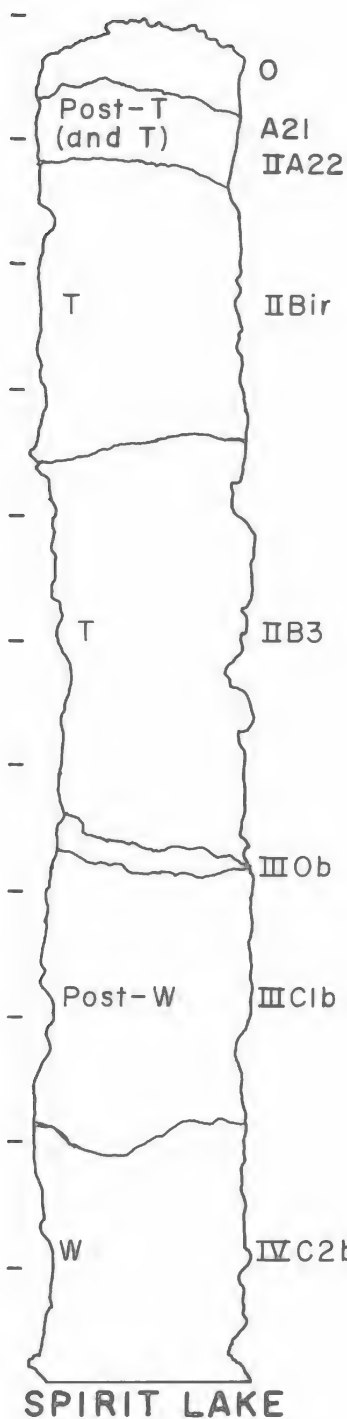


D

SPIRIT LAKE

WEST BLACKTAIL

Figure 3. Soil monoliths (A, B, and C) with Mount St. Helens layer T and (D) with West Blacktail ash. The ticks at the left of each profile are at 1-dm intervals.



Profiles sampled between the 150- and 200-km arcs have weak Bir horizons. In the western part of the area sampled, A2 horizons have developed chiefly from layer W, which is sufficiently old that disturbance is characteristic. In the eastern part of the area, A2 horizons have developed chiefly from layer T, which is nearly continuous on gentle slopes if fires have not been catastrophic. The characteristic horizon sequence is O1-O2-A2-IIBirb, with the A2 developed from layer T (Fig. 3-C). We found only one area with both layers T and W present, in which case the sequence is O1-O2-A21-II02b-IIA22b-IIIBirb.

We also collected surface pyroclastic samples northeast into the Okanogan Highlands and north to the Canadian border (Fig. 1). In several sites sampled at a distance of 25 to 75 km directly south of Glacier Peak and also in a few sites west of these, the surface pyroclastic material is commonly Mount St. Helens layer Y forming the A2 of Spodosols. In areas immediately south of Lake Chelan and in many parts of the Okanogan Highlands, the silty surface ash has the same mineralogy as does Glacier Peak pyroclastic material. Although we observed this ash over a large area, we did not trace it to its source. In places it overlies coarse-textured Glacier Peak pumice, but more often it covers one of several lithic materials.

Spodosols on both sides of the 49th parallel, between 114° and 121° longitude, are developed in part from another pyroclastic layer that has not been traced to its source. The horizons developed from it are variable. In several Canadian profiles the layer forms an A2 over a lithic IIBirb, but in others it produces an A2-Bir sequence. In the area of occurrence of West Blacktail ash (Fig. 2) this unidentified layer forms a IIA23b horizon.

Summary

Fallout from the 1800 A.D. eruption of Mount St. Helens, in southwestern Washington, was traced 185 km toward the northeast. This pyroclastic layer T correlates in terms of age, particle size distribution, and mineralogy with the West Blacktail ash, which occurs in northeastern Washington, northern Idaho, and northwestern Montana. There is a 160-km gap between the known areas of occurrence of these two layers. Recognition of the A2 horizons in Spodosols is enhanced by the presence of thin layers of these pyroclastic materials.

Acknowledgments

Some of the soil monoliths were collected for us by John Aarstad, Richard Dingle, Roald Fryxell, Glen Greene, Lorraine Greene, Richard Mack, Polly Naffziger, Shiro Okazaki, Robert Pfister, Robert Reed, Melvern Rupp, Norman Sprout, Robert Woollard, and A. L. van Ryswyk.

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The Microtool Industry of the Ice Mountain Microblade Phase

Introduction

The Ice Mountain Microblade Phase is currently known from three sites—IaTq-1, HlTs-1, and HlTs-2. These components are located in the Stikine-Tahltan region of the Ice Mountain Archaeological Project area (Fig. 1). This area is presently defined as running from 130°00' to 132°30' west longitude, and 57°15' to 58°15' north latitude.

As a result of surveys conducted in the Telegraph Creek area of northern British Columbia by W. Workman in 1967 and B. C. Gordon in 1968, a program of testing and excavation was undertaken during the summers of 1969 and 1970. A preliminary report on the results of the 1969 field season is now available (Smith, 1970).

Description of the Region

The project region consists of the Stikine and Tahltan river valleys which have been cut and dissected by glacial and fluvial action; the relief ranges from 150 to 1200 m above sea level in extremely rugged terrain.

Extensive and continuing Quaternary vulcanism and continental, intermontane cordilleran, and valley glaciation are the most important geomorphological factors in the recent development of the region and the project area. Vulcanism has been the subject of intensive investigation in recent years (Souther, 1965, 1966, 1967, 1970). However, there has been very little analysis of surficial deposits of glacial origin. Some preliminary work has, however, been done by Johnston (1926), Kerr (1934, 1936, 1938), and Mathews (1947).

The valley of the lower Stikine (most westerly) has an annual rainfall of 2540 mm (100 inches) or more, while that of the interior Stikine ranges from 381 mm (15 inches) to 635 mm (25 inches) per year. Temperature extremes, ranging from -51 to 35°C (-60 to 95°F), are not normally of any great duration.

Soil development ranges from luvisolic and podzolic to chernozemic, supporting both deciduous and coniferous vegetation. The rate of regional soil formation is quite slow, not an abnormal subarctic situation, the chief depositional agents being mass wasting, colluvial movement, and irregular fluvial action. Site erosion is primarily a fluvial-aeolian activity.

Existing biotic and recovered osteological evidence indicates a relatively uniform distribution of the faunal assemblage through Neoglacial times (post 6000 BP) at least. The assemblage is relatively large for the project area and is of the type found in the Boreal-Montane Coniferous Forest and Alpine Biome of Shelford (1963).

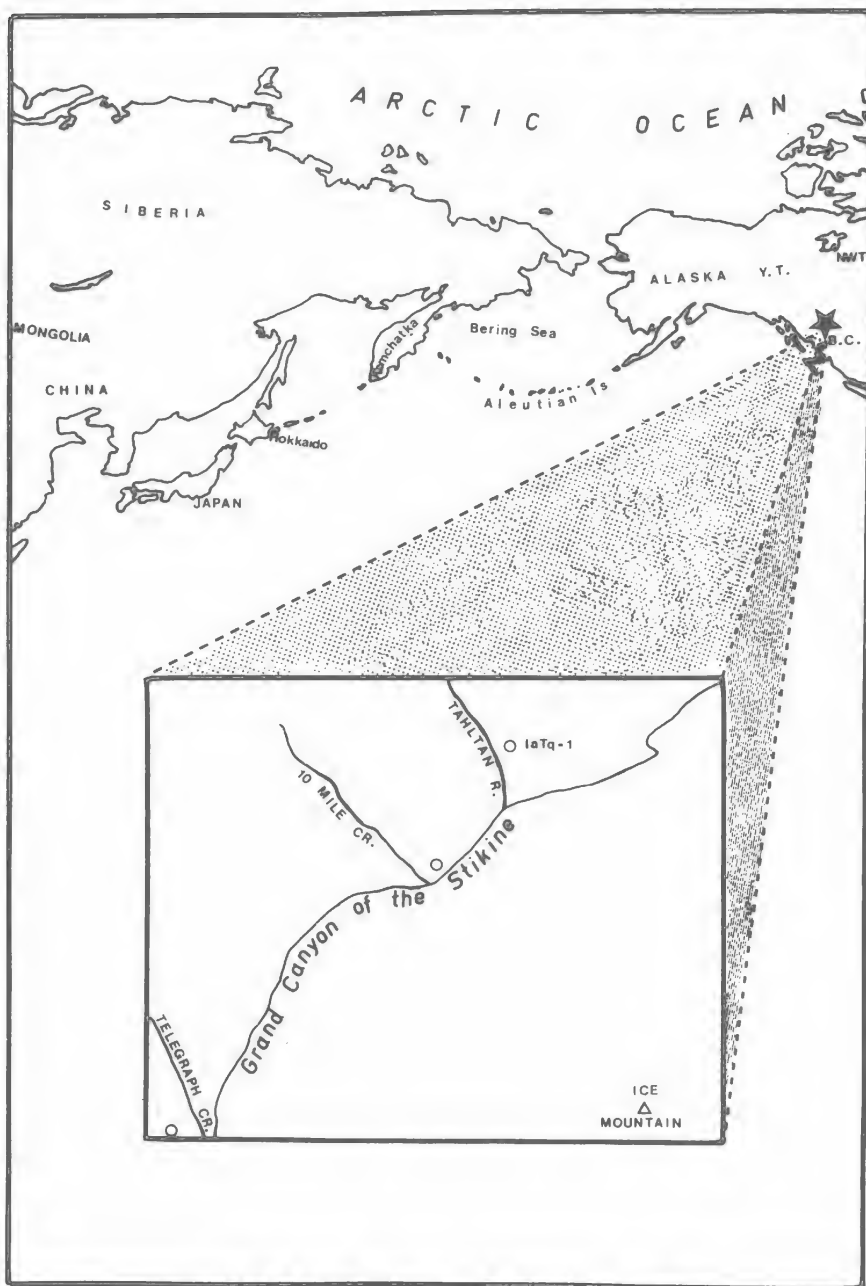


Figure 1. East Asia and Northwest America showing the sites in the Cassiar District mentioned in the text.

The Ice Mountain Microblade Phase has been placed preceding a series of components, the most recent of which comprise the Tahltan Phase and represent the historic and protohistoric Athabaskan occupation; the intermediate period is poorly

understood. The Microblade Phase is preceded by at least two groups of components currently referred to as Cordilleran and Pre-Cordilleran I and tentatively assigned to the period from 10,000 to 30,000 BP. These components have been only tentatively described (Smith, 1970, 1971).

Chronology

Figure 2 graphs the relative frequency distribution of microblades and microblade cores, compared with the year of field collection as an index of sample reliability. Fifty-five percent of the microblades collected in 1970 reproduced hydration values developed for the 1969 collection, while only 7 percent fell outside the previous distributional range at the early end of the continuum. The remaining 38 percent filled out the previously defined distribution at intervals between 3500 and 1800 years BP and between the later 1000 to 500 years BP, thus reconfirming the presence of the latter. Based upon relative frequency, the peak industrial use of obsidian in the manufacture of microblades occurred at about 4500 BP, having been initiated prior to 10,000 BP, and terminated at 500 BP. Interpreted literally, there are two clusters of hydration dates, the earlier extending from about 11,000 to 2000 BP and the later from 1000 to 500 BP.

The hydration time scale applied in Figure 2 is founded on a provisional local rate of 1.4 microns²/1000 years BP. This specific rate was suggested by Koch (1965) based upon his study of obsidian samples from the Onion Portage site in the interior of Alaska. This rate is significantly faster than the rate of 0.82 microns²/1000 years BP derived originally by Friedman and Smith (1960). The faster rate of 1.4 has also been supported by Davis' cooperative studies with Donald Clark, National Museum of Man (Ottawa), of Koyukuk River obsidian use sites (Davis, pers. comm., 1970, 1971).

Description of the Microtool Industry

Recovery and Field Analysis

Following recovery by surface collection and excavation, where the specimens were recorded with precise locational and provenience data, the following division into categories was carried out in the field laboratory: (1) used amorphous blades; (2) waste amorphous blades; (3) amorphous blades exhibiting clear retouch and/or form associated with possible specific manufacturing technique and/or use, such as microburins, microspokeshaves, etc.; (4) used flakes; (5) waste flakes; (6) flakes with retouch or form as above. This field procedure was based on apparent visual differences and was to facilitate analysis once the research laboratory at the University of Calgary was in possession of the specimens. Earlier studies of the author were important in deriving the procedure and its criteria (Mead and Smith, 1968).

Analysis and Recognition

Analytical procedure was designed to recognize attributes which would aid in the establishment of categories defined on the basis of form and technology. Such categories would then be further examined in an attempt to determine possible and/or probable uses of the artifacts involved in these form-technological categories. Thus, we established type-variety groups which in addition to having primary definition in terms of form and manufacture would contain a component of information with some degree of probability in terms of utility.

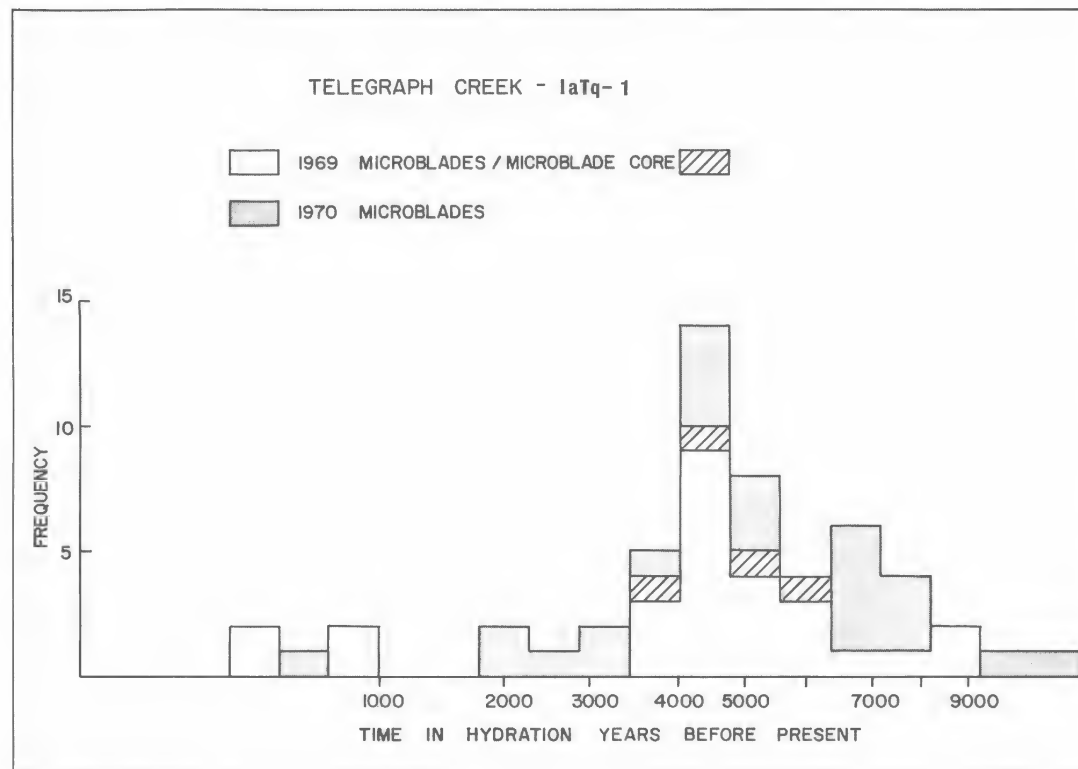


Figure 2. Graph of the relative frequency of occurrence of microblades and cores uncovered at site IaTq-1 during 1969 and 1970. Temporal values obtained through obsidian hydration analysis as described in text.

Pit	N7E1												N8E1												Trench A Section 1				Trench A Section 2				Trench A Section 3				N8E5				N8E6				N9E6				N9E5				TOTAL
Level	2	3	4	5	6	2	3	4	5	6	7	8	9	2	3	4	5	2	3	4	5	2	3	4	2	3	4	2	3	4	5	6	7	2	3	4	5	6	2	3	4	5	6										
Field Lab Categories																																																					
Used Amorphous Blades	2	20	24	28	21	2	20	10	19	16	1			4	4	23		15	19	18	5	43	21	266	73	21	33	301		38	41	3	321	153	11		1	162	83	30	1	1	1854										
Waste Amorphous Blades	3	57	44	5		1	19	15	9	10					10			3		1	2		9		2				4	4		14	6				21	9					248										
Retouched/Form Amorphous Blades		2				1	3	5	2	3					1	1						1	1				2	3					3	2			1	2					33										
Used Flakes	1		10	45	49	3	10	4		5				4	31	21		10	27	19	4	121	155	255	169	25	69	322	144	66	46	3	362	635	33	1	232	156	45	6	2		3091										
Waste Flakes	10	61	69	18	10	18	48		12	9			1	3	7	11		3	9	2	1	9	11	50	9	17		39	30	25	14		80	64	8		37	30	15	1			731										
Retouched/Form Flakes	3	4	7	7		3	9	2	1	1				4	3		1					4		4		1	1	1	3	2		6	14	4		7	6	2					100										
TOTAL	19	144	154	103	80	28	109	36	43	44	1		1	11	46	69	1	29	58	39	12	180	187	585	251	63	107	666	175	136	107	6	786	874	56	2	460	286	92	8	3		6057										

Figure 3. Artifacts sample examined by the authors.

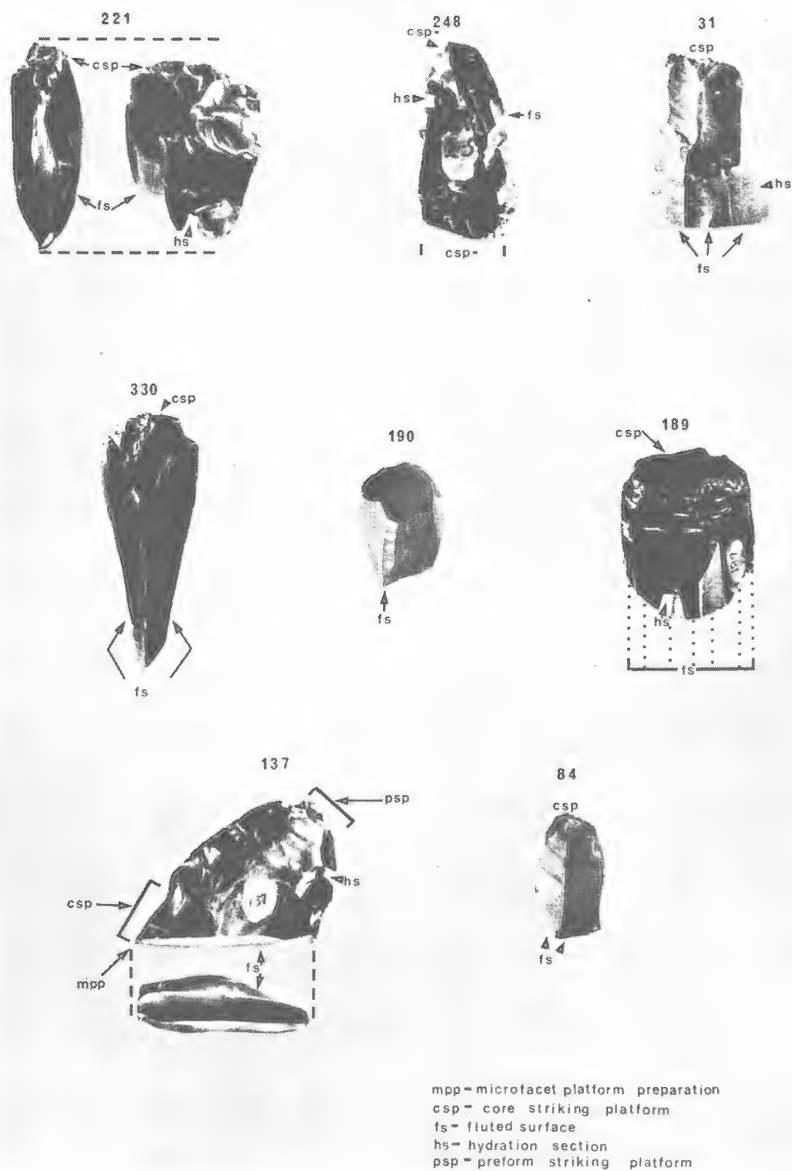


Figure 4. Microblade cores from site IATQ-1. These are the diagnostic specimens of the Ice Mountain Microblade Phase.

Schematic of Laboratory Method

- Analysis: I —Rigorous visual (low power optical) examination of all specimens for formal and technological attributes, specifically as given by Reeves (1970).
- Recognition: (A) Consistent Form Category
1. General attributes
2. Specific attributes clusters
(B) Consistent Technological Pattern Category
1. General attributes
2. Specific attributes clusters
- Analysis: II —Microscopic examination of artifacts for wear patterns to establish regularities related to function, specifically as given by Semenov (1970).
- Recognition: (A) Type-variety groups defined on the basis of form-technological categories with a functional information component of high confidence.

Type: Variety Groups

The purpose of the following is the illustration of methodology; we shall present a summary description of specimens taken from a series of type-variety groups rather than a comprehensive review. Four major groups have been recognized and each exhibits a series of internal variations. We shall discuss representative specimens of the best known varieties within each group.

Group 1—Thin flakes or amorphous blades (<5 mm) with one tool aspect where the angle formed by two faces is the critical characteristic (147 specimens recovered).

Specimen: MT #12 (Figure 5a)

Formal Attributes: The dorsal-ventral surfaces of the flake are determinate on this obsidian microtool and have been arbitrarily assigned on the basis of patination (considered dorsal cortex). Two lateral faces intersect at a right angle to form the tool aspect; the flake is trapezoidal in plan view.

Technological Attributes: Both the dorsal and ventral faces are unworked and the flake exhibits no retouch. Two lateral faces were formed as a product of flexion snapping. The angle shows little wear with the exception of microflake removal on the ventral corner; adjacent to the microflake scar at the angle is further microflake removal on lateral face 'A,' probably a result of use, extending 5 mm. Microflake removal on lateral face 'B' occurs on the ventral surface 4 mm from the angle. No crushing was detected on either face near the angle. The majority of striations on the ventral surface run perpendicular to the angle. A second and third set of striations run perpendicular to the lateral edges; no clear pattern of superposition can be discerned with regard to these sets of striations.

The dorsal side of the flake is patinated exhibiting a set of strong and predominate striations running across the entire surface at acute angles to lateral faces 'A' and 'B.' Presumably, these striations were formed before this microtool was manufactured; a second set of striations is superimposed and runs perpendicular to the angle.

Functional Extrapolation: It would appear as if the angle has been used as the working aspect of an engraving tool on wood or bone; the ventral surface of the flake being positioned in a forward position prior to movement into and through the material to be worked; lateral face 'A' being distal to the hand of the operator. The

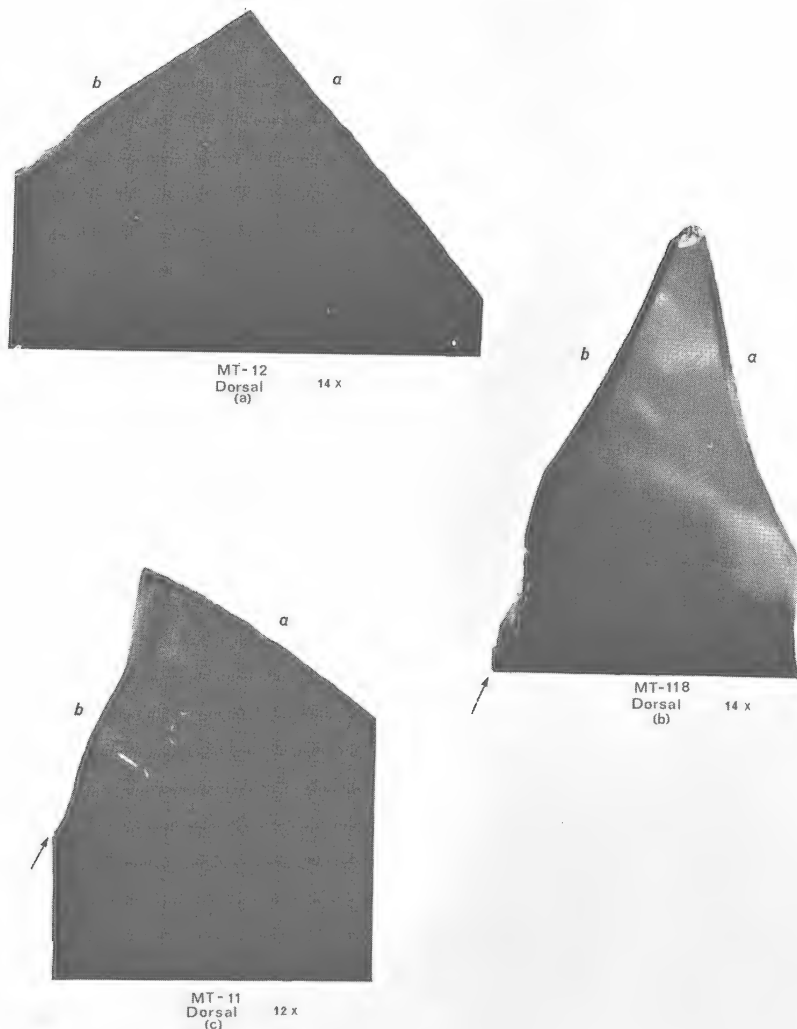


Figure 5. Tool aspect group I.

relative lack of striations, due to use in this fashion, on the dorsal surface near the angle seems to these writers to indicate that the tool was used in a primarily unidirectional manner.

Specimen: MT #118 (Figure 5b)

Formal Attributes: The microtool in this specimen is formed as a consequence of the intersection of two lateral faces on an amorphous blade trapezoidal in plan view. The

ventral and dorsal surfaces of the blade are determinate; the dorsal surface exhibits two blade scars and an arris; both surfaces are otherwise unworked.

Technological Attributes: Lateral face 'A' was produced as a function of flexion snapping while lateral face 'B' is the product of a burin spall removal originating near the proximal margin. The angle shows considerable wear in the form of crushing. Microflaking was recorded at the dorsal corner of the angle. Both of the lateral edges which form the angle exhibit microflaking and wear dorsally and ventrally. No striations are apparent on the lateral faces themselves, although they are present on the dorsal and ventral surfaces adjacent to lateral edge 'B.' These striations are oriented perpendicularly to that edge.

Functional Extrapolation: We believe that the evidence points to the conclusion that the angle has been used as the working aspect of an engraving tool. Lateral face 'B' was probably positioned parallel to the material to be worked with the angle in a proximal and forward position. The striation pattern is interpreted as indicating unidirectional movement of the microtool.

Specimen: MT #11 (Figure 5c)

Formal Attributes: The specimen is an amorphous blade, rectangular in plan view, having an arris over the entire length of the dorsal surface. The ventral surface exhibits a bulb or percussion and concentric ripple marks. No other retouch occurs.

Technological Attributes: As was the case for specimen 118, the blade has two lateral faces, one formed as a result of flexion snapping and the other by a burin blow directed at the proximal margin of the blade. The angle shows little wear with the exception of microflaking on the ventral corner. Adjacent to this microflake removal is further microflaking along the dorsal surface in association with lateral face 'A' extending 7 mm. Similar removal occurs along the dorsal area for 5 mm near lateral face 'B'; along lateral face 'A' ventrally for 5 mm; and, along lateral face 'B' ventrally for 7 mm. This microflake removal seems to be the result of use rather than intention. Crushing is visible along lateral face 'A' ventrally, and along lateral face 'B' dorsally, near the angle.

The majority of striations occur near the angle and are oriented perpendicularly to lateral face 'A' and parallel to lateral face 'B' dorsally; ventrally the striations are predominantly oriented parallel to lateral face 'A' and at right angles to lateral face 'B.' A second set of striations is evident on the ventral surface although no clear pattern of superposition can be discerned; most of these are oriented parallel to a line bisecting the angle.

Functional Extrapolation: It would appear that the angle has been used as the working aspect of an engraving tool, lateral face 'B' being positioned parallel to the material to be worked with the angle in a forward position. Alternatively, lateral face 'A' could have been positioned parallel to the material with the angle in a proximal position. The tool would have been moved toward and away from the operator, respectively; probably both methods were employed.

Group 2—Thin flakes or amorphous blades with one tool aspect where the presence of a notch is the critical characteristic (16 specimens recovered).

Specimen: MT #121 (Figure 6a)

Formal Attributes: The dorsal and ventral surfaces of this flake are determinate; the ventral surface is concave and the positive bulb of percussion is present. The flake is pentagonal in plan view. A notch 5 mm in diameter exists on the distal end of the flake and forms the working aspect of this microtool.

Technological Attributes: The dorsal surfaces of this flake were worked prior to the manufacture of the microtool; the ventral surface is unworked. The notch was formed as a product of dorsal retouch along the edge. Microflaking as a result of use is evident only on the dorsal area adjacent to the notch. Crushing is present but of a limited degree and isolated to the extreme margin of the notch. The ventral surface

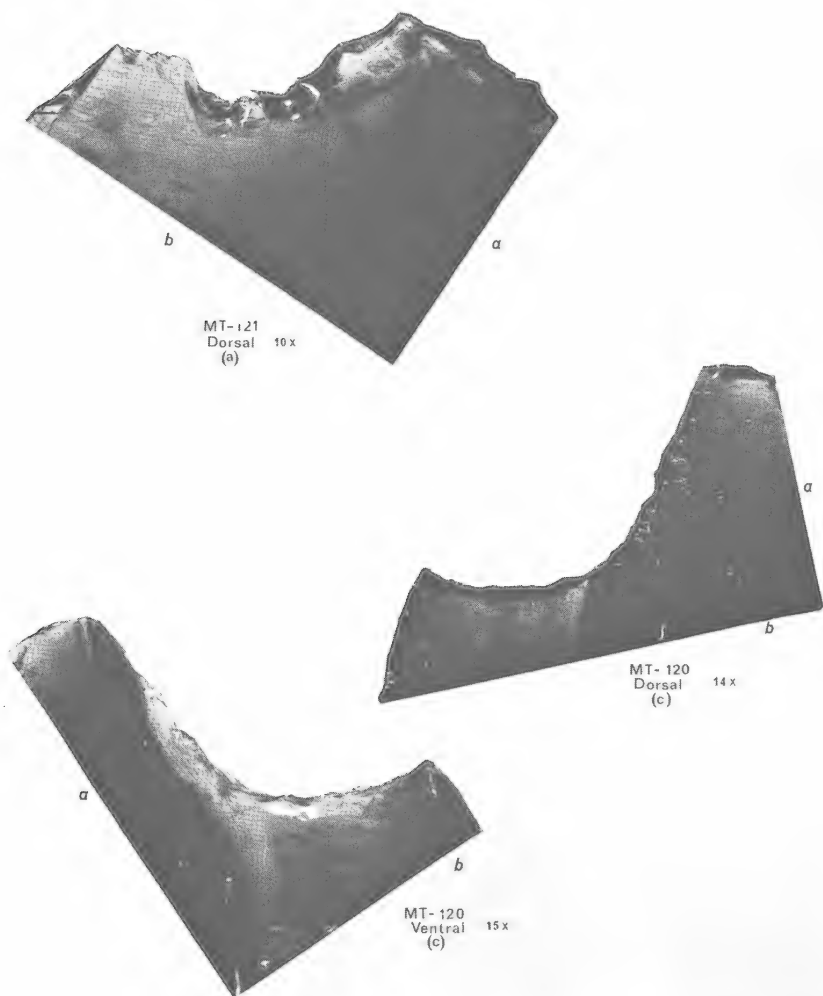


Figure 6. Tool aspect group II.

adjacent to the notch shows striations perpendicular to a line drawn across the notch from margin to margin of the lateral edge.

Functional Extrapolation: From the above evidence, it would appear that the notch has been used as the working aspect of a spokeshave-like tool. The ventral surface of the flake being positioned next to the material to be worked with the notch in a distal position and the flake held by the operator at an acute angle relative to the surface to be worked, unidirectional movement, probably toward the operator given the character of the striation orientation, seems indicated. This tool may have been used in the manufacture of such things as bone needles and other small cylindrically styled tools.

Specimen: MT #120 (Figure 6b and 6c)

Formal Attributes: This microtool is made on an amorphous blade, pentagonal in plan view, with clear dorsal and ventral surfaces. The blade is roughly triangular in cross and longitudinal section.

Technological Attributes: Two blades were removed from the dorsal surface leaving an arris and two scars prior to microtool manufacture. Neither the dorsal nor the ventral surface was subsequently retouched. A thick lip was formed on the dorsal surface of the distal end as a consequence of torsion snapping. A notch was formed naturally in the area between the lateral edge of the blade and the lip; this notch was extended and deepened through use. There is slight microflaking on the dorsal side of the notch and extensive microflaking on the ventral side of the notch along the entire arc. Considerable crushing is evident along the notch margin. Extensive striations in the dorsal area of the blade adjacent to the notch are noted. These striations appear unrelated to the notch in terms of origin.

Functional Extrapolation: It would appear that the notch has been used as the working aspect of a spokeshave tool. The dorsal surface of the microtool would have been placed next to the material to be worked with the notch in a distal position relative to the operator's hand. The microtool appears to have been used in a unidirectional fashion primarily; movement toward the user seems likely.

Group 3—Thin flakes or amorphous blades with one tool aspect where edge retouch is the critical characteristic (29 specimens recovered).

Specimen: MT #71 (Figure 7a)

Formal Attributes: The dorsal surface is convex; the ventral surface is concave and retains the positive bulb of percussion. The flake is rectangular in plan view and exhibits secondary retouch along the distal margin.

Technological Attributes: Large flake scars predominate on the dorsal surface of this flake; the ventral surface is unworked. The retouched distal margin of the flake exhibits crushing. Striations parallel to this tool edge appear on both the ventral and dorsal surfaces. A second set of striations perpendicular and adjacent to the retouched edge appears on the ventral surface.

Functional Extrapolation: From the evidence above, it would appear that the retouched edge has been used in at least two ways. First, as a cutting implement;

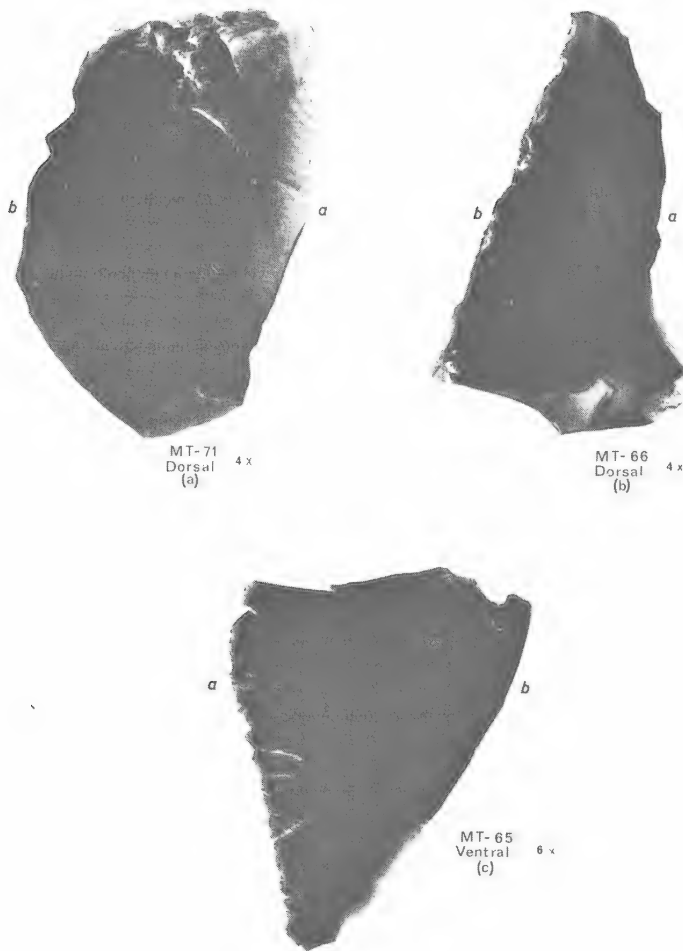


Figure 7. Tool aspect group III.

parallel striations, crushing, and microflaking along both dorsal and ventral surfaces at the lateral edge could be explained as a function of this type of use. Second, the perpendicular striations (ventrally) and the microflaking (dorsally) could be seen as a function of scraping; the concave ventral surface was probably placed next to the material to be worked. This specimen is believed to represent the multipurpose single component variety of microtools.

Specimen: MT #66 (Figure 7b)

Formal Attributes: This microtool is formed on an amorphous blade, triangular in plan

view, with distinguishable dorsal and ventral surfaces. The bulb of percussion is absent on this fragment although concoidal ripple marks are clear and complete over the ventral surface; fissures radiate across the proximal half (ventrally). A small blade scar can be seen on lateral face 'B' and is followed by secondary retouch which forms the tool aspect of the blade.

Technological Attributes: The otherwise unworked ventral surface exhibits a series of superimposed flake scars along the proximal margin; these scars are 5 mm in length. The dorsal surface is completely worked. Microflaking seems to have been the result of intentional pressure or percussion directed at right angles to the proximal edge. Limited microflaking is evident along the ventral surface adjacent to the retouched edge of lateral face 'B.' The dorsal area near lateral face 'B' is characterized by extensive crushing.

Striations are extensive on the ventral surface running parallel and tangential to the retouched edge. Similarly oriented striations are found dorsally adjacent to the retouched edge.

Functional Extrapolation: This specimen seems to these writers to have been a multipurpose tool used primarily for cutting and scraping. The major attributes considered by the writers were the striation pattern, the character of the microflaking, and the extent of the crushing.

Specimen: MT #69 (Figure 7c)

Formal Attributes: The microtool was formed on an amorphous blade, triangular in plan view, with a clear concave ventral surface. The bulb of percussion is present. The convex dorsal surface exhibits a blade scar near lateral face 'B.' The tool aspect consists of a ventrally retouched area of lateral face 'B.'

Technological Attributes: No flaking of either surface is evident other than that described above. Limited microflaking can be seen along the dorsal surface of the retouched edge. Ventral microflake removal is recorded at the midpoint of the retouched edge. Extensive crushing along the retouched edge and the microflaking seem related to use rather than intention.

Striations appear on the ventral surface near the area of retouch; these striations are oriented perpendicularly to the tool edge and have their origin in its use. Striations appear dorsally, however, the character of the retouch indicates that these striations were formed on the blade prior to the manufacture of the tool aspect.

Functional Extrapolation: The investigators believe that the retouched edge has been used as the working aspect of a scraping tool, possibly in the preparation of hides. The ventral surface adjacent to the tool aspect was probably placed against the surface to be scraped at an acute angle and moved in a primarily unidirectional fashion.

Group 4—Thin flakes or amorphous blades where the presence of two or more tool aspects is the critical characteristic (51 specimens recovered).

Specimen: MT #10 (Figure 8a)

Formal Attributes: The dorsal surface of this essentially flat and trapezoidal (plan view) flake is extensively worked. The ventral surface is unworked and exhibits a bulb of

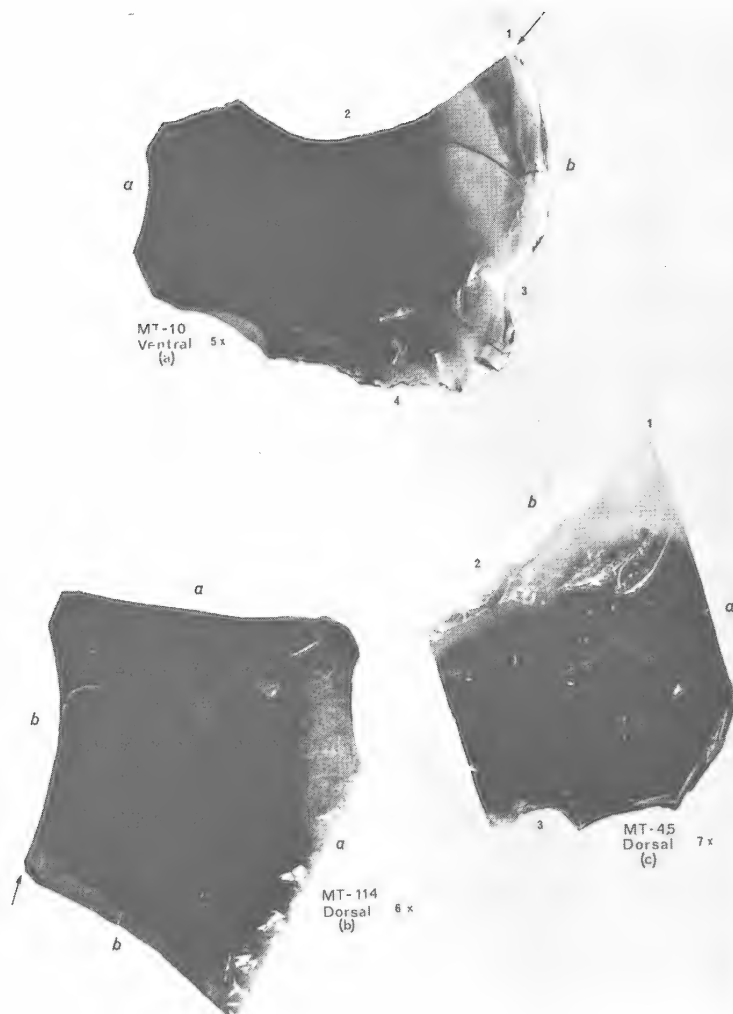


Figure 8. Tool aspect group IV.

percussion. Four tool aspects appear on this flake: (1) an angle formed by the intersection of a flake edge and a lateral face; (2) a notch on the distal margin; (3) a notch on the lateral face opposite the distal margin; and (4) secondary retouch along the lateral face 'B' on the dorsal surface adjacent to it.

Technological Attributes: A burin spall was removed from the distal margin of the flake as a product of pressure or percussion directed against the left lateral margin of the flake. The angle thus formed exhibits extensive crushing and microflaking; this crushing and microflaking extends for 4 mm along the left lateral margin. Striations parallel to a line bisecting the angle appear on the ventral surface adjacent to the angle.

The left lateral margin has been retouched along its dorsal surface.

Near the proximal end of the flake a notch was formed on the left lateral margin ventrally (retouch flake scars appear on the ventral surface). Microflaking occurs within the notch dorsally. Ventrally striations in association with the notch were recorded running in a perpendicular fashion to the margin. A second and extensive set of striations appears both dorsally and ventrally, although no nonrandom pattern could be discerned.

Functional Extrapolation: It is possible that the angle has been used as the working aspect of a perforating tool; initially the flake would have been held so that the angle contacted the surface to be pierced. Little or no twisting motion is believed to have been involved in the process of perforation. The left lateral margin seems to have been used as the working aspect of a scraping tool, the dorsal surface having been placed next to the surface to be worked.

The notch on the left lateral margin may have been used as the working aspect of a spokeshave-like tool. It would appear as if the flake was held in a position such that the ventral surface was adjacent to the material to be worked and at an acute angle.

The distal notch is similar and probably fulfilled a similar function. This notch may have been moved in a bidirectional fashion with both surfaces having been placed at one time or another against the material to be worked.

Specimen: MT #114 (Figure 8b)

Formal Attributes: The flake is roughly rectangular in plan view, having some flake scars on the convex dorsal surface. The concave ventral surface is unworked; the bulb of percussion is missing although the concentric ripple marks are present. Two tool aspects (angles) appear on this flake and will be referred to as proximal and distal.

Technological Attributes: Distal Angle: Lateral face 'B' has been forced as a result of burin spall removal by pressure applied to the left lateral midpoint of the flake; force was directed distally. Lateral face 'A' was formed as a product of torsion snapping. These two faces intersect at an acute angle. Lateral face 'A' exhibits retouch extending 3 mm from the angle. Microflake removal is visible on the angle and on both faces 'A' and 'B' and the surfaces adjacent to them. Crushing also appears on both edges of lateral faces 'A' and 'B.' Two sets of superimposed striations appear on the ventral surface; the first approximating a parallel pattern with respect to a line bisecting the angle and the second set intersecting the bisecting line more or less at right angles. Both striations and microflaking appear to be the result of use.

Proximal Angle: Lateral face 'B' was formed as the product of torsion snapping and lateral margin 'A' by retouching along the dorsal surface. Microflake removal is found adjacent to lateral margin 'A' and lateral face 'B' dorsally and ventrally. The angle also exhibits crushing and microflaking.

Two sets of superimposed striations were observed on both surfaces. These originate as a product of use, run at right angles and/or parallel to a line bisecting the angle.

Functional Extrapolation: Both the proximal and distal angles appear to have been used as perforating tools. In this case, the writers believe that the process of perforation was characterized by a clockwise or counterclockwise twisting motion.

Specimen: MT #45 (Figure 8c)

Formal Attributes: This flake is trapezoidal in plan view with determinate dorsal and ventral surfaces and exhibits three tool aspects. Two lateral faces intersect to form one; a second aspect consists of retouching on a lateral margin and a third is seen in the presence of a notch in the proximal margin.

Technological Attributes: The ventral surface is unworked while the dorsal surface is scarred by prior flake removal. Lateral margin 'B' was modified by retouching; lateral face 'A' is a product of torsion snapping. The two edges intersect at an acute angle and form a working aspect of the flake. Microflaking is evident on the angle.

Striations appear on the ventral surface near the angle oriented parallel to lateral

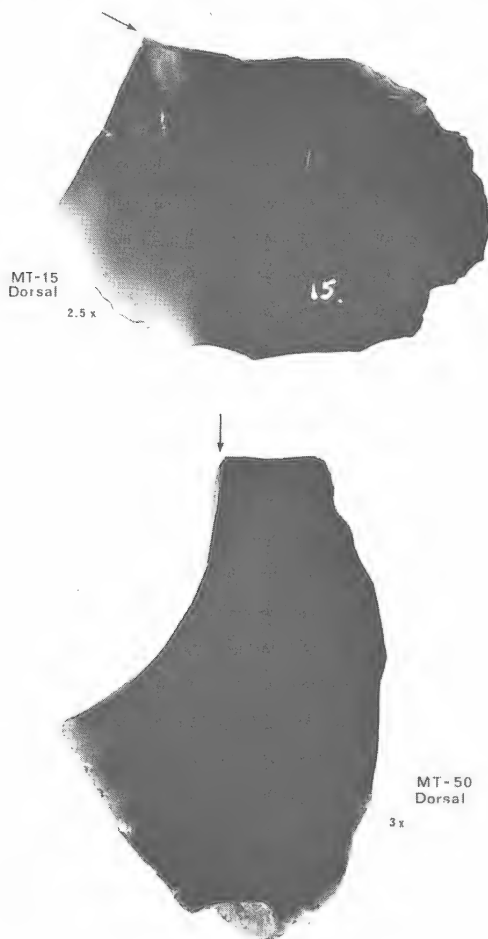


Figure 9. Near microtool formed on snapped flake exhibiting burin blow.

face 'A'; the surface of this lateral face also shows striation running parallel to its edges. Microflaking appears on the surface of lateral face 'A' originating from pressure applied in the area of the ventral surface adjacent to the margin. Crushing is visible on this face as well.

Striations are recorded running perpendicular to the retouched edge (lateral margin 'B') on the ventral surface; slight microflaking and crushing is visible on the dorsal surface near this edge.

Retouch on the dorsal surface of the proximal aspect of the flake brought about the formation of a notch. Crushing and microflake removal is evident on the ventral side of the notch margin. Striations on the ventral surface are perpendicular to the notch margin. Another set of randomly oriented striations appears on both surfaces but does not appear to be a product of notch utilization.

Functional Extrapolation: The angle aspect of the flake seems to have been used as an engraving tool, the lateral face 'A' having been placed adjacent to the surface of the material to be worked with the angle in a forward position prior to movement. The retouched edge (lateral margin 'B') was probably utilized as a scraper of some sort; the flake would have been held in such a way as to have placed the ventral surface against the material to be scraped at a steep acute angle. The notch was probably another spokeshave-like tool and could have been employed in the manufacture of wood and bone tools; the ventral surface of the flake would have been held against the material to be worked.

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National Park Wildlife Management Policy: A Case Study in Decentralized Decision-Making

This paper is based on a study of National Park Service wildlife management policy at Rocky Mountain National Park. The summers of 1963 and 1964 were utilized gathering data at the above park under a Resources for the Future, Inc., grant. The three main sources of data were: (a) personal interviews, (b) public documents (especially wildlife rangers' and wildlife specialists' reports), and (c) correspondence. The central problem of the Park's wildlife policy was the elk and mule deer populations, which at times increased in numbers beyond the carrying capacity of the limited winter range. This increase consequently affected the vegetation, with detrimental effects in some cases. This paper deals with *how* decentralized decisions were made to deal with this problem by field men and specialists. The premise is that specialists were dominant over field men in decision-making.

A partial policy vacuum was assumed because only a minimum of direction was available from the broad and idealistic wildlife policy statements of the National Park Service. The NPS Act of 1916 stated "... to conserve the scenery and the natural and historical objects and wildlife" and stipulated that the Secretary of the Interior "... may also provide in his discretion for the destruction of such animals and such plant life as may be detrimental to use of said parks ..." (Tolson, 1933). However, the National Park Service developed a policy of wildlife protection based on the "vanishing wildlife concept" of the early 1900's, *i.e.*, sanctuaries. The Leopold report (1965) noted little major change during the first 40 years.

With the absence of hunting and predators and with favorable environmental conditions, elk and deer populations began to increase rapidly in Rocky Mountain National Park. The majority of RMNP reports of the Park personnel noted a gradual increase in the number of these animals. Severe vegetation damage took place on the limited winter range on the eastern side of the Park with reports of starvation of animals. Damage to crops and forage outside the Park by migrating animals was also noted.

Wildlife reports by Park personnel and non-park specialists were assumed to be the key to the decentralized policy decision-making. Prior to 1930 (the Park was established in 1915) all wildlife data were contained in superintendents' reports to the Director of the National Park Service. Early superintendents were delighted with the profusion of wildlife. Wildlife management consisted of rough wildlife censuses with no reference to vegetation or habitat and with predator control programs to avoid killing of elk and deer (until the early 1920's). Yet, in 1931, in the first official wildlife management report, Chief Ranger John McLaughlin commented, "The range generally is in very poor condition" (McLaughlin, 1931). Almost every wildlife report after 1930 until the early 1960's reported similar poor range conditions.

Nevertheless, no mention was made of poor range conditions in the superintendents' reports from 1915 to 1930.

Regarding policy, McLaughlin (1931) noted, "All possible effort should be made to arrive at the numbers of animals on the range and its carrying capacity. A more definite policy will depend on future developments and the range recovery." The superintendent's report of 1931, which was based on McLaughlin's report, noted, "The winter range problem of the Park elk and deer is rapidly assuming serious proportions. Regulation of the increase in the herds based on the carrying capacity of the winter range may be necessary" (Annual Report, 1931). In subsequent wildlife reports, attempts to estimate the numbers of animals and the carrying capacity of the winter range were usually mentioned, as well as broad philosophical policy discussions. Finally, the numbers of 400 elk and 800 deer were suggested by an unknown official in the early 1940's as a "guestimate."¹ These figures were accepted as official figures in subsequent reports.

Washington, D.C. and regional wildlife specialists also made special studies of the Park during the 1930's. In general, they concluded with Park wildlife reports recognizing the large numbers of animals and the consequent poor condition of the winter range. With the exception of a recommendation to acquire more winter range, concrete recommendations were not presented. In fact, in a special report in 1931, Joseph Dixon, a National Park Service biologist, commented: "The other alternative to securing more winter range would be to reduce the present stock in the Park and this to the writer would seem inadvisable" (Dixon, 1931). In a publication in 1933 on wildlife in national parks, however, Dixon and two other wildlife biologists made a policy statement that wildlife should remain within the carrying capacity of the winter range (Wright *et al.*, 1933). In another special report in 1939, Dixon urged a reduction in wildlife to the carrying capacity of the winter range (Dixon, 1939).

In general, the Park wildlife reports of the 1930's recognized the problem of elk and deer overpopulation and of the deterioration of the winter range. The reports also acknowledged that some type of control was needed. Enclosed vegetative study plots were established as controls to demonstrate the impact of intensive foraging on surrounding unprotected areas. In 1940, Fred Packard, a wildlife specialist, recommended that the herds of animals should be reduced by 50 percent. He also stated that several Washington, D.C. high-ranking National Park officials agreed with this recommendation (Packard, n.d.). However, Park officials declined to make a definite commitment; they stressed further observation relative to vegetation and carrying capacity.

In 1943, Victor Cahalane, a wildlife biologist, called a conference with Park officials after he had completed a special study. In conference, the Park staff concurred with Cahalane in regard to the destruction of the winter range and the need for direct reduction (shooting of animals by park rangers). Cahalane noted that the Director of the National Park Service, Drury, disagreed with direct reduction unless it proved a definite necessity. As a result of the conference, a report was issued to Drury which justified direct control in 1943 where abnormal damage was occurring

¹ One of the problems confronting wildlife rangers and specialists was to present an unknown approximate number of animals for the carrying capacity of the winter range. Various interviews revealed that an unknown official had made the above estimates and that these estimates had been incorporated in reports from the early 1940's. This was also the case for Yellowstone National Park, where a round number of 5000 was suggested for the northern elk herd relative to reduction programs.

by concentrations of animals (Anonymous, 1943).

Relative to the reduction decision of February 22, 1943, Superintendent David Canfield (who chaired the conference) noted that the rangers had first recognized the overgrazing condition with the debarking of aspen. He stated, "It seemed obvious to me that what the rangers were showing was beyond question in validity. Other key individuals did not show up until some years later after we had evidence pointing to the definite conclusion that the elk-deer population was overabundant and the forage situation was becoming critical." Canfield believed that it was group decision in the conference.² However, several National Park Service officials associated with the problem thought that the field men were given an unofficial "go ahead" from high-level officials before making the reduction-decision recommendation.

Significantly, an "outside wildlife specialist" initiated the conference and helped solve the problem, although the facts were obvious to the Park staff. Also, the NPS Regional Office at Omaha, Nebraska was behind the park request for reduction and helped to facilitate it through channels of the Director and the Secretary of the Interior on approval. Although the request was finally approved, some opposition did occur. Associate Director Hillory Tolson (1947) noted, "As you are well aware, this office (Washington, D.C.) has a strong dislike for 'reduction programs' either inside or adjacent to the national parks." Also, some park rangers did not support the program because they were eager for autonomy in deciding solutions to park problems.

Control measures were implemented from the mid-1940's to the early 1960's with park rangers shooting "surplus" animals. An annual herd reduction was maintained for the majority of these years. A typical policy statement of the 1950's was made by Stanley E. Broman, one of the numerous park rangers who was assigned to the wildlife program: "In carrying on the work of my predecessors, I recommended that the number of ungulates on the eastern slope be maintained at below the estimated carrying capacity to allow the range to build up."³ Each year the number of animals to be controlled became progressively fewer as minor improvements were reported in range conditions. The reduction of ungulates in the 1950's was relatively light in numbers as contrasted to heavier numbers in the late 1940's. In reports, many wildlife rangers pointed out that continued harassment of the elk and deer was necessary to keep them away from the more depleted areas of the range.

Public opinion was often strongly opposed to the reduction program with different reactions of superintendents to this pressure. Superintendent James Lloyd was said to dislike the reduction program because of some negative public responses. In a memorandum in 1957, Lloyd stated, "I have heard some complaints locally that the wildlife is not in the Park as it should be, due to too much reduction. I feel we should check if this were possible" (Lloyd, 1957). Under a sliding rule concept, that is, no definite quota, Lloyd encouraged rangers to take only small numbers of elk and deer. Consequently, large reductions had to be undertaken after he left the Park in 1961. In a reply to Lloyd's memorandum in 1957, Cole, a wildlife specialist, noted that the animals had erupted and had to be controlled to protect the habitat (Cole, 1955). This had little effect on Lloyd's sliding rule concept although it might have

² Personal correspondence with David H. Canfield, Santa Fe, New Mexico, January 14, 1964.

³ Personal correspondence with Stanley E. Broman, Staff Park Ranger (wildlife), National Park Service, Southwest Region, Santa Fe, New Mexico, June 22, 1964.

served as a detriment to possible termination of reduction resulting from negative public opinion.

In 1963, the reduction program was terminated. Wildlife reports indicated a general improvement in the range although some sections still indicated damage by sedentary herds. Live trapping of the animals for release outside the Park was utilized for further reduction. Although expensive and difficult, the live trapping method encountered little public opposition. It did reduce pressures for public hunting in the Park by the state people who wanted hunters rather than rangers to shoot the surplus animals. Trapping was advocated and implemented by Neal Guse in 1963. He was assigned as the first permanent wildlife biologist (wildlife management background) to the Park. Previous rangers from 1930 to 1963 had a variety of backgrounds and conducted the wildlife program along with other duties. Guse has summarized the history of elk and deer in Rocky Mountain National Park (Table 1).

The broad and idealistic wildlife policy of the National Park Service emphasized the sanctuary concept. Thus years of dissatisfaction with range conditions, as documented in wildlife reports, had to be built up before specific policy or action occurred (1930-1944). Moreover, with the innovation of population reduction, pressures of administrators and public opinion obviously effected a decrease in the reduction program as well as its termination. Many rangers who submitted wildlife reports confined themselves to what Lindblom describes as "incrementation" (Lindblom, 1959).⁴ By this, Lindblom was referring to a process of adding relevant and "safe" recommendations in marginal areas without making radical suggestions such as a large reduction request. Thus the policy of the reports remained passive and kept a conservative appearance, with idealistic discussions of wildlife policy interspersed.

March and Simon note that governmental field reports can be compared to book reports with inferences drawn from broad generalizations rather than from the evidence itself (Price, 1959). In this sense, there is the implication that rangers could tell the superintendent what he wanted to hear as well as the consideration that a ranger would not recommend anything (particularly radical policy changes) which a superintendent would not support. Documentation revealed that some superintendents, as well as Washington officials, were not sympathetic with reduction programs.

Although field men had the discretion for specific policy recommendations, little consideration was given to making a radical recommendation such as population reduction. Although early reports did involve discussions of policy for wildlife, it remained the role of specialists to innovate and to encourage a radical recommendation of reduction. Obviously the wildlife rangers had been aware of this alternative for some time. Growing dissatisfaction with increasing poor range conditions was noted in the reports with a definite identification of the problem. Yet the wildlife rangers did not make a recommendation for reduction. Some of the factors in operation were: (a) the various superintendents who did not indicate a strong support, (b) job

⁴Lindblom states: "It is a matter of common observation that in Western Democracies public administrators and policy analysts in general do largely limit their analyses to incremental or marginal differences in policies which are chosen to differ only incrementally. They do not do so, however, solely because they desperately need some way to simplify their problems; they do so in order to be relevant. Democracies change their policies almost entirely through incremental adjustments. Policy does not move in leaps and bounds."

TABLE. 1. A Brief History of Elk and Deer in Rocky Mountain National Park.¹

History of the area in relation to wildlife populations, management practices and various studies as summarized from the official records of Rocky Mountain National Park. Primary emphasis of study is on the interaction between deer and elk and their environment, especially vegetation, but also with other animals such as beaver, bighorn, and including man.

Year	Est. Population		No. Reduced		Remarks
	Elk	Deer	Elk	Deer	
1800's	"large herds"		"many"		Killed for food, sport, and market.
1860's	"mod. plentiful"				Beginning of major decline in herd numbers.
1890	"near extinction"	"scarce"			Last elk (bull) reported killed at mouth of Big Thompson Canyon.
1912-14		"scarce"			Total of 69 elk released from Yellowstone NP. Only approximately 30 survived.
1915	30	600			Rocky Mountain National Park established.
1919	80				Col. State Game Refuge established along Park's east boundary.
1920-25	"increase"				Many writers coincide the elk increase with the bighorn decline.
1926	200	3000			Predator control practices (1917-1926) ended in the Park.
1930	330	3600			Serious barking of aspen by elk first reported. Continued heavy horse-cattle grazing and hay cutting in the large meadows.
1931-32	400	2500			All domestic animals removed by land purchase except Moraine Park.
1933-34	375	3000			Twelve enclosures (20' x 20') established on forage types to study range trend.
1936-39	1210	2600			Critical browse condition reported. Peak of deer numbers on winter range, 1021 counted. Spring 1939.
1941-43	1525	1750			Peak of elk numbers on winter range. Spring 1944 count—766.
1944-45	1000	1400	301	113	First major elk and deer control program.
1949-50	1272	969	340	100	Second major elk and deer control.
1950-53	700	900	297	329	Total of 297 elk and 329 deer reduced.
1954	700	900			Signs of minor total range recovery.
1954-58	700	900	180	59	Total of 180 elk and 59 deer taken. Last year of deer control.
1959	700	800	30	0	Removal of 1870 deer in unit #20.

(continued)

TABLE 1 (continued)

Year	Est. Population Elk	Deer	No. Reduced Elk	Deer	Remarks
1959-62	1100	600	205	0	Removal of 1408 deer in unit #20. Long-range management plan begun.
Present	1200	600			Range continues to improve except for isolated damage from sedentary herds.

security with concern or wanting to remain aloof from policy or politics, (c) Washington, D.C. office and public opinion opposition to reduction with emphasis on a sanctuary concept or protection of wildlife, (d) the individual's mental picture of past conditioning decisions (of protection for some), and (e) avoidance of unpopular or unpleasant decisions. These factors were also in operation for decreasing and finally terminating reduction. The total implication, however, is that the wildlife rangers would not recommend anything concrete that the superintendent might not support.

However, growing dissatisfaction was documented in the various reports as a "safe" or factual type of inference with emphasis on a need of wildlife reduction. Also, the trend of the wildlife management reports illustrated the impact of the relatively new science of wildlife management technology, from a qualitative description to quantitative data, especially for wildlife populations and vegetation. Nevertheless, the role of the "outside" wildlife specialist to recommend policy remained paramount, regardless of dissatisfaction inferences and supportive data. Thus the specialist reiterated the wildlife ranger's observations with an addition of obvious policy, *i.e.*, "reflectors." The specialists, however, were assured that the reduction recommendation would be supported by some high-ranking NPS officials in the Washington, D.C. office.

Although the "right" atmosphere was possibly available for the Park decision, with a receptive superintendent and with dissatisfaction in wildlife reports, a specialist, Cahalane, had to initiate the conference for the decision which was noted as "group" decision. The group decision thus took the pressure off the superintendent as well as wildlife rangers. Moreover, as the innovator, the specialist could be held responsible for the decision rather than the Park staff, given that the superintendent had final responsibility. Also, as previously noted, the specialist did have informal support and encouragement from the Washington, D.C. office. The field men, in this situation, reported their dissatisfaction and had obvious data, but did not make a definite policy decision or recommendation. They did, however, provide a force and background (as well as a possible informal but unidentified influence) for the reflector or outside specialists who dominated the decision-making.

Discussion and Conclusions

As far as policy decisions are concerned, there is no evidence that inferences are made through the collection of data from the field. The so-called "scientific method" presumably undertaken by experts which includes the collection and measurement of biological facts, in the end, does not result in the formation of any legitimate theory upon which any intelligible policy may be based. Policy seems to result by the *infusion*

of values into data with emphasis on the specialist in a supportory value role for latent values of field wildlife personnel and park administrators.

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Trace Element Analyses of Columbia River Water and Phytoplankton¹

Introduction

Chemical analyses of water are common but there is a paucity of information regarding detailed elemental analyses of phytoplankton, particularly on a seasonal basis. Silker (1964) has presented activation analyses of Columbia River water and Cushing (1964) has reported on earlier analyses by conventional techniques. Davis *et al.* (1958) published data on mineral composition of several Columbia River organisms, including green algae. Several workers (Angino *et al.*, 1969; Sreekumaran *et al.*, 1968; and MacCrimmon and Kelso, 1970) have published data on trace element concentrations in various rivers. Boyd and Lawrence (1967) reported data on the mineral composition of several freshwater algae, and Merlini *et al.* (1969) published data on elemental composition of freshwater microplankton determined by activation analysis.

To provide baseline data for future ecological studies of trace element cycling in the Columbia River ecosystem, water and phytoplankton samples were collected upstream from the Hanford Atomic Works Project at five "ecologically significant" times of the year for analysis by neutron activation techniques. The five times selected were: (1) November, during the fall phytoplankton bloom, (2) February, during mid-winter, (3) April, during the spring bloom, (4) June, during the summer high water period, and (5) August, during the stable summer conditions. Elements analyzed in the phytoplankton were Ag, Br, Co, Cr, Cs, Fe, Hg, K, Na, Rb, Sb, Sc, Se, and Zn. In addition to these elements, As, Au, Cu, Mn, and U were measured in the water. Costs of sample analyses by neutron activation precluded more frequent sampling; however, monthly samples of water and phytoplankton were collected and analyzed for Ca, Mg, Na, K, Zn, Cu, and P by standard methods for comparison by these readily available techniques.

The purpose of this paper is twofold: (1) to describe the elemental composition of the Columbia River water and phytoplankton during the period of November 1968 to August 1969, as analyzed by neutron activation, and (2) to compare these data with those obtained from samples submitted to a routine analytical laboratory where the analysts were unfamiliar with the sample constituents or particular problems involved with sampling and processing. The paper also presents data on concentration factors of the elements in the phytoplankton.

Methods and Materials

Water for activation analyses was collected from beneath the water surface in special, precleaned 80 ml Nalgene containers, frozen immediately with Dry Ice, and kept

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frozen until activated. Water for standard analyses was collected at the same place in precleaned polyethylene bottles and kept in a refrigerator until analyzed.

Phytoplankton was collected in a special net (Nitex #73, 73 μm pore openings) constructed with nonmetallic materials to minimize contamination. The phytoplankton was also frozen until activated.

Basic aspects of the irradiating procedures and subsequent separation and gamma spectroscopy of the neutron activated water samples have been described by Rancitelli and Tanner (1969). Activated phytoplankton was radioanalyzed with the same system.

Analyses by standard methods were as follows: Na and K were determined by flame photometry; Ca, Mg, Cu, and Zn by atomic absorption; and P by the phosphomolybdate complex with ascorbic acid reduction (Murphy and Riley, 1962).

Results and Discussion

Water

Tables 1 and 2 present the results of analyses of water samples by neutron activation and standard techniques, respectively. It is difficult to discern any over-all seasonal

TABLE 1. Element concentrations (ppb) in Columbia River water as determined by neutron activation analysis.

Element	11-14-68	2-12-69	4-24-69	6-11-69	8-14-69
Ag	0.50	<0.01	<0.01	3.03	<0.01
As	2.5	1.4	2.9	2.6	2.4
Au	0.030	<0.005	<0.005	<0.005	<0.005
Br	5.6	5.4	5.4	4.9	4.1
Co	0.02	0.04	0.22	0.06	0.09
Cr	0.4	<0.1	0.1	0.2	<0.1
Cs	0.35	0.03	0.02	0.03	0.03
Cu	2.6	0.6	1.5	1.0	1.1
Fe	13.	<10.	62.	24.	17.
Hg	<0.1	<0.1	0.2	<0.1	0.1
K	1190.	560.	1060.	920.	990.
Mn	2.8	5.4	43.8	9.4	11.0
Na	2200.	1365.	2900.	1880.	2100.
Rb	3.5	0.4	0.9	1.1	1.3
Sb	0.24	0.43	1.04	0.30	0.43
Sc	0.002	0.001	0.015	0.003	0.006
Se	0.2	0.2	0.1	0.2	0.1
U	0.7	0.5	1.0	1.0	0.7
Zn	8.	44.	6.	8.	6.

trends from the data in Table 1. Data in Table 2 reveal a slight seasonal decrease of most elements during the high water period of May to July. These trends are consistent with those reported by Cushing (1964). A few analyses in Table 1 seem unreasonable when compared with other values, *e.g.*, Ag on 6/11/69, Co on 4/24/69, Cs on 11/14/68, Mn on 4/24/69, and Zn on 2/12/69, but a few exceptions seem to be typical of most extensive chemical analyses. The best data to compare these values with are those of Silker (1964). Comparing the ranges of values shows that Na, Mn, U, and perhaps Co and Sc appeared to be present in higher concentrations in the present study. Values for other elements are similar. Cushing (1964) presented analyses of several elements in Columbia River water performed by nonactivation techniques, and these can be compared with the data in Table 2. Cu is slightly higher in the present study but all other elements show no differences.

TABLE 2. Element concentration (ppm) in Columbia River water as determined by standard methods.

Date	Ca	Mg	Na	K	Zn	Cu	P
11-14-68	15.75	4.37	1.65	.6	<.010	<.010	.0404
1-17-69	17.00	4.80	2.02	.65	.013	<.010	.0521
2-12-69	24.0	4.5	2.08	.6	.053	<.010	.0809
3-12-69	25.0	5.43	1.9	.86	.094	.076	.0356
4-24-69	19.80	5.06	2.30	1.40	.031	.009	.056
5-22-69	14.60	3.45	1.60	.70	<.010	<.010	.0375
6-11-69	11.75	3.12	1.25	.55	<.010	<.010	.0272
7-16-69	17.80	3.86	1.26	.62	.026	.009	.101
8-14-69	18.50	4.60	1.62	.77	.031	.023	.026
9-17-69	18.50	3.90	1.90	<.50	.0117	.007	.028
10-15-69	18.85	4.10	1.92	.83	.0276	.007	.054
11-13-69	18.70	4.33	1.98	.82	.012	.005	.038

It is of considerable interest to compare like data in Tables 1 and 2 since this gives a comparison of the two analytical techniques. This can be done for the elements Na, K, Cu, and Zn. Considering over-all ranges, Cu analyses by standard techniques were considerably higher than those by activation analyses; Na, K, and Zn were within reasonable limits. Individually, Na and K tended to be higher when analyzed by activation analysis and Cu and Zn higher by standard techniques, although zinc values were duplicated the best of any elements both in the water and in the phytoplankton (see below).

Phytoplankton

The net phytoplankton of the Columbia River is dominated by *Asterionella formosa* and *Fragilaria crotonensis* with significant populations of *Tabellaria* sp., *Synedra* sp., and *Melosira* sp. present.

Tables 3 and 4 present the analyses of the phytoplankton samples by neutron activation and standard techniques, respectively. As with the water, insufficient data are available in Table 3 to show seasonal trends although analyses of several elements were lowest on the 2/12/69 sampling. A tendency toward lower values during high water (May-July) is present in the data in Table 4, although inconsistencies in the results confuse the picture.

Much greater variability exists in the samples when concentrations of particular elements are examined. No comparable data on a seasonal basis are available, so it is

TABLE 3. Element concentrations (ppm dry wt) in Columbia River net plankton as determined by neutron activation analysis.

Element	11-14-68	2-12-69	4-24-69	6-11-69	8-14-69
Ag	0.93	0.22	0.45		0.44
Br	17.7	5.43	20.8	6.19	6.35
Co	9.11	2.15	10.6	11.0	7.73
Cr	22.8	5.36	24.3	29.4	19.0
Cs	2.11	0.56	2.52	2.18	2.08
Fe	19200	5000	24400	24400	18100
Hg	0.56	0.32	2.9	0.35	0.02
K	10700	5600	23000		19400
Na	8000	2100	7100	14700	6600
Rb	69.0	17.7	58.9	44.2	138
Sb	0.79	0.36	1.50	2.85	1.06
Sc	5.98	1.59	7.10	8.01	5.62
Se	1.77	0.55	0.73	1.16	1.66
Zn	1310	1170	980	830	1360

TABLE 4. Element concentrations (ppm dry wt) in Columbia River net plankton as determined by standard methods.

Date	Ca	Mg	Na	K	Zn	Cu	P
11-14-68	4000	6060	233	506	1520	279	10620
1-17-69	4080	5040	252	3300	1110	59	3630
2-12-69	3380	3100	275	4290	1230	48	5990
3-12-69	4400	4260	280	5520	1280	82	5260
4-24-69	704	7770	900	5020	900	55	7200
5-22-69	962	4580	381	1990	731	68	5310
6-11-69	511	6210	374	2920	719	42	5330
7-16-69	688	4860	620	3060	1042	32	2060
8-14-69	794	5410	454	3830	1360	75	3020
9-17-69	910	6400	760	4700	1280	36	3640
10-15-69	905	7160	330	3610	1460	60	2600
11-13-69	862	8360	516	4120	1530	60	2600

not known whether fluctuations in concentrations of the magnitude seen here are to be expected. In Table 4, there also appear to be errors in analysis, *e.g.*, the over-all change in Ca, and the results for Cu, P, and K on 11/14/68.

Considerable discrepancy arises when like analyses on the same data are compared from Tables 3 and 4. This can be done for the elements Na, K, Zn. Analyses of Zn by the two methods were in good agreement; however, measurements by neutron activation revealed much higher values for Na and K, sometimes as much as 40 times (compare Na on 6/11/69). Differences of this magnitude led to a critical review of sample handling, since no machine errors could be detected. It was subsequently found that the service laboratory doing the standard analyses was using hydrochloric acid to dissolve the phytoplankton and assuming that everything went into solution despite the fact that considerable residue remained. To investigate this further, a sample of phytoplankton was irradiated, submitted to the service laboratory which treated it as usual, and then both the solution and the residue were radioanalyzed. Table 5 presents the percentage composition of the two portions and reveals that a considerable amount of mineral matter was not being taken into solution. This is particularly evident for Na, but even if we apply an 87 percent correction factor to the Na values in Table 4, they do not always approximate the values in Table 3. This resulting difference is unexplainable at the present time. (It was found that further treatment of the samples with hydrofluoric acid resulted in better dissolution of samples dominated by siliceous diatoms.)

TABLE 5. Elemental distribution (percent of total) after wet chemical dissolution of net plankton with hydrochloric acid.

Element	Solution	Residue
Br	61	39
Cr	50	50
Co	85	15
Cs	60	40
Fe	76	24
Hg	94	6
La	82	18
Na	13	87
Rb	40	60
Sb	33	67
Sc	52	48
Se	59	41
Zn	85	15

Potassium-to-sodium ratios are often used in examining chemical variability in biological samples. The K:Na ratios for the phytoplankton samples are more variable for the standard methods (2.17 to 15.6) than for the activation analyses (1.34 to 3.24). K:Na ratios for the water data showed a range of 0.29 to 0.61 for standard analyses and from 0.37 to 0.54 for activation analyses; on several dates the two were essentially identical. If a constancy of this ratio is indicative of meaningful analyses, then it appears that the phytoplankton analyses for Na and K by standard techniques are faulty. If the Na values are corrected on the basis of the data in Table 5 and the K:Na ratios are recomputed for phytoplankton by standard analyses, we obtain a range of 0.28 to 2.02, which is much more constant than the one from the uncorrected data.

Merlini *et al.* (1969) quotes Barnes (1956) as stating that there was little or no bibliography on the elementary composition of freshwater microplankton and further states that little has changed. Boyd and Lawrence (1967) present extensive data on analyses of 14 genera of algae and also allude to the paucity of information of this type. It would be difficult and perhaps meaningless to compare absolute concentrations of elements in algae and phytoplankton from different water bodies. The mineral composition of the algae will reflect to a large extent that of the ambient media. Species present will also differ as will their demand for the various minerals. Nevertheless, an attempt should be made to put the present data into some perspective. Merlini *et al.* (1969) present the only data we could find giving elemental analyses of phytoplankton measured by neutron activation techniques. The phytoplankton in the lake they studied consisted of two species of diatoms and one blue-green alga. They found values of 1790, 209, 4433, and 72 ppm for Ca, Na, K, and Mn, respectively. If we calculate the K:Na ratio for this sample we obtain a value of 21.1 which is considerably different from those found in the present study. No water data are presented. The reader is referred to the paper of Boyd and Lawrence (1967) for an extensive list of analyses of individual algal genera; no attempt will be made to compare it with the present data.

Concentration Factors

Concentration factors are a means of expressing the degree to which an organism concentrates a given element over that in the ambient water. They are calculated by dividing the concentration of the element in the organism per gram wet weight by the concentration per ml of water. However, it is obvious that values of this sort derived from analytical measurements of concentrations are only as good as the original analyses. This fact, together with the analytical discrepancies mentioned in the preceding section, should be kept in mind when interpreting the concentration factors presented below, particularly those for Na and K by standard methods.

Table 6 presents the concentration factors calculated from the neutron activation analyses. The phytoplankton concentrate Sc and Fe from the water to a greater degree than the other elements. Na is concentrated the least.

Table 7 gives the concentration factors calculated from the standard analyses, uncorrected for the dissolution problem mentioned above since only a single test of this was performed; therefore, the Na values obviously are too low. Of the elements measured by these techniques, P and Zn are concentrated to the highest degree and Ca the least. Algae are known to concentrate P metabolically to a high degree when it is present in nonlimiting amounts, as it is in the Columbia River. Zn, on the other hand, is accumulated mainly by surface adsorption (Cushing and Rose, 1970). Watson *et al.*

TABLE 6. Concentration factors of Columbia River net plankton determined from neutron activation analyses.

Element	11-14-68	2-12-69	4-24-69	6-11-69	8-14-69
Ag	620	>7000	>15000		>15000
Br	1050	335	1280	420	517
Co	152000	18000	15900	61700	28700
Cr	19000	>17900	81000	49000	>63000
Cs	2000	6300	42000	24000	23000
Fe	492000	>76700	131000	339000	355000
Hg	>1900	>1100	4800	>1200	70
K	3000	1900	7200		6500
Na	303	510	126	2600	105
Rb	6600	14800	21800	13400	35400
Sb	1080	280	480	3200	810
Sc	995000	530000	160000	890000	312000
Se	3000	900	2400	1950	5500
Zn	54600	8900	54500	34600	75600

TABLE 7. Concentration factors of Columbia River net plankton determined from standard method analyses.

Date	Ca	Mg	Cu	Zn	Na	K	P
11-14-69	85	460	>9300	>50700	47	280	87600
1-17-69	80	350	2000	28500	42	1700	23200
2-12-69	47	230	>1600	7700	44	2400	24700
3-12-69	59	260	360	4500	49	2100	49300
4-24-69	12	510	2000	10000	130	1200	42900
5-22-69	22	440	2300	>24400	79	950	47200
6-11-69	15	660	1400	>24000	100	1800	65300
7-16-69	13	420	1200	13400	160	1600	6800
8-14-69	14	390	1100	14600	93	1700	38700
9-17-69	16	550	1700	36500	133	>3100	43300
10-15-69	16	580	2900	17600	58	1500	16000
11-13-69	15	640	4000	42500	87	1700	22800

(1970) have published concentration factors for ^{65}Zn and ^{32}P by Columbia River phytoplankton. Their values are of about the same order of magnitude as those found for stable Zn and P in the present study.

It is of some interest to speculate as to how certain trace elements are found associated with the phytoplankton. Several of the elements in Table 3 are known to be trace elements concentrated by biological processes in plants, *i.e.*, Ag, Br, Cs, K, Na, Rb, Se, and Zn. The concentrations of other elements, *i.e.*, Co(?), Cr, Sb, and Sc, are not known to be concentrated by biological processes so some other source of association may be indicated. Physical adsorption and entrapment of colloidal mineral matter by the gelatinous matrix of the diatoms are possibilities. To investigate this further, we calculated from the literature what the ratios of these elements would be in geological parent material assuming a 50 percent granite and 50 percent diabase mixture. We then compared the ratios of these with those in the phytoplankton and found similar values for Co, Cr, Sb, and Sc. Many of the rare earths (not shown in Table 3) were also found in the same ratio as in geological material in a single plankton sample.

The main result of this study is to demonstrate the importance of involving the personnel charged with analyses of environmental samples with all aspects of the sampling techniques, sample constituents, sampling problems, and processing of the samples. The data also demonstrate the superiority of neutron activation analyses over

more conventional techniques in detection of micro quantities of trace elements in biological samples.

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A Bibliography of Oregon Ornithology (1935-1970), with a Cross-Referenced List of the Birds of Oregon

In order to document recent advances in the knowledge of the birds of Oregon, an extensive bibliography has been compiled and is presented here. This survey covers literature which appeared from 1935 to 1970. We felt that the ornithological literature prior to this period was adequately covered by Gabrielson and Jewett (1940. *Birds of Oregon*, Oregon State Monographs No. 2, Oregon State College, Corvallis, Oregon) in their classic work on the birds of Oregon. We have attempted to include all literature citations of behavioral, ecological, distributional, and taxonomic studies which were conducted in the state or which used specimens or data from the state.

Most articles from newspapers, popular magazines, and governmental bulletins are excluded from this bibliography as are articles from strictly local publications of natural history societies and other similar organizations. A few references from these sources are included if they contain pertinent information not available in any other publication. Such publications as *American Birds*, Bent's *Life Histories of North American Birds*, and many of the popular field guides are so extensive in their coverage that they serve as handy references in themselves and are therefore not included. Except for those dealing with subfossil remains, literature which deals strictly with fossil birds is not included.

The references cited are numbered and listed in alphabetical order by author. Following this is a phylogenetic listing of bird species known to occur in Oregon (Bertrand and Scott. 1971. *Checklist of the Birds of Oregon*, O.S.U. Bookstores). After each species are listed the numbers of the references which contain information about that particular species. Those species for which we found no references are followed by an asterisk.

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Name

ORDER GAVIIFORMES

Family Gaviidae

- Common Loon *Gavia immer* 98, 147
- Yellow-billed Loon *Gavia adamsii**
- Arctic Loon *Gavia arctica**
- Red-throated Loon *Gavia stellata* 147

ORDER PODICIPEDIFORMES

Family Podicipedidae

- Red-necked Grebe *Podiceps grisegena* 223, 241
- Horned Grebe *Podiceps auritus* 96, 147, 234, 240, 241
- Eared Grebe *Podiceps caspicus* 98, 147, 165
- Western Grebe *Aechmophorus occidentalis* 147, 252
- Pied-billed Grebe *Podilymbus podiceps* 96, 98, 132, 147, 252, 329

ORDER PROCELLARIIFORMES

Family Diomedidae

- Short-tailed Albatross *Diomedea albatrus* 359
- Black-footed Albatross *Diomedea nigripes* 149, 298, 299, 301, 362, 363, 366
- Laysan Albatross *Diomedea immutabilis* 103, 251, 254, 298, 301

Family Procellariidae

- Fulmar *Fulmarus glacialis* 298, 301
- Pink-footed Shearwater *Puffinus creatopus**
- New Zealand Shearwater *Puffinus bulleri**
- Sooty Shearwater *Puffinus griseus* 301, 363
- Slender-billed Shearwater *Puffinus tenuirostris* 301
- Manx Shearwater *Puffinus puffinus**
- Scaled Petrel *Pterodroma inexpectata* 355

Family Hydrobatidae

- Fork-tailed Petrel *Oceanodroma furcata* 100, 241, 298, 301, 363
- Leach's Petrel *Oceanodroma leucorhoa* 86, 100, 298, 301, 363

ORDER PELECANIFORMES

Family Phaethontidae

- ²Red-billed Tropic Bird *Phaethon aethereus* 363

Family Pelecanidae

- White Pelican *Pelecanus erythrorhynchos* 98, 147, 157, 165, 239, 241, 252, 323
- Brown Pelican *Pelecanus occidentalis* 241

Family Phalacrocoracidae

- Double-crested Cormorant *Phalacrocorax auritus* 8, 98, 64a, 132, 147, 157, 165, 252, 290, 291
- Brandt's Cormorant *Phalacrocorax penicillatus* 100
- Pelagic Cormorant *Phalacrocorax pelagicus* 100

Family Fregatidae

- Magnificent Frigate Bird *Fregata magnificens* 164

ORDER CICONIIFORMES

Family Ardeidae

- Great Blue Heron *Ardea herodias* 35, 42, 64a, 96, 98, 115, 132, 147, 165, 252, 290, 291, 320, 338
- Green Heron *Butorides virescens* 38, 40, 65, 89, 96, 115, 124, 147, 180, 201, 252, 289
- Cattle Egret *Bubulcus ibis* 230
- Common Egret *Casmerodius albus* 96, 98, 147, 157, 165, 237, 241, 278, 294, 320, 338
- Snowy Egret *Leucophoyx thula* 154, 240, 241, 345
- Louisiana Heron *Hydranassa tricolor* 305
- Black-crowned Night Heron *Nycticorax nycticorax* 35, 42, 64a, 98, 165, 252
- Least Bittern *Ixobrychus exilis* 241
- American Bittern *Botaurus lentiginosus* 96, 147, 165, 252

Family Threskiornithidae

- White-faced Ibis *Plegadis chibi* 165, 241, 297

ORDER ANSERIFORMES

Family Anatidae

- Mute Swan *Cygnus olor**
- Whistling Swan *Olor columbianus* 82, 96, 147, 157

² Not cited by Bertrand and Scott (1971)—no records within 25 miles of the coast.

Trumpeter Swan *Olor buccinator* 241, 309
 Canada Goose *Branta canadensis* 13, 42, 61, 96, 98, 147, 151, 157, 161, 165, 194, 209, 222, 241, 252, 290, 291, 325, 365, 367
 White-fronted Goose *Anser albifrons* 96, 98, 147, 241
 Snow Goose *Chen hyperborea* 96, 98, 147, 215, 234, 240
 Ross Goose *Chen rossii* 183, 240
 Blue Goose *Chen caerulescens* 234, 240
 Fulvous Tree Duck *Dendrocygna bicolor* 1
 Mallard *Anas platyrhynchos* 4, 35, 42, 82, 96, 98, 132, 147, 165, 252, 329
 Black Duck *Anas rubripes* 199
 Gadwall *Anas strepera* 35, 64a, 96, 147, 165, 252, 329
 Pintail *Anas acuta* 35, 82, 85, 96, 98, 132, 147, 160, 165, 362, 363, 364
 Common Teal *Anas crecca* 70, 160, 200
 Green-winged Teal *Anas carolinensis* 70, 96, 147, 363
 Blue-winged Teal *Anas discors* 96, 147, 154, 165, 250, 356
 Cinnamon Teal *Anas cyanoptera* 64a, 87, 96, 147, 165, 250, 252, 329, 356
 European Widgeon *Mareca penelope* 147
 American Widgeon *Mareca americana* 58, 64a, 82, 96, 147, 152
 Shoveler *Spatula clypeata* 64a, 96, 147, 165, 240
 Wood Duck *Aix sponsa* 96, 98, 126, 132, 147, 216, 266, 294
 Redhead *Aythya americana* 85, 165, 252, 329
 Ring-necked Duck *Aythya collaris* 147, 241, 242, 272
 Canvasback *Aythya valisineria* 85, 96, 98, 147
 Greater Scaup *Aythya marila* 234
 Lesser Scaup *Aythya affinis* 96, 98, 147, 241
 Tufted Duck *Aythya fuligula* 272
 Common Goldeneye *Bucephala clangula* 96, 147
 Barrows Goldeneye *Bucephala islandica* 98, 126, 234, 241
 Bufflehead *Bucephala albeola* 64a, 90, 96, 126, 129, 147, 240, 241
 Old Squaw *Clangula hyemalis* 240
 Harlequin Duck *Histrionicus histrionicus* 107, 241
 White-winged Scoter *Melanitta deglandi* 219
 Black Brant *Branta nigricans* 48, 82, 83, 87, 111, 222, 307, 316
 Emperor Goose *Phalacrocorax canagica* 147, 296, 307
 Surf Scoter *Melanitta perspicillata* 60, 198, 220, 224, 278, 324
 Common Scoter *Oidemia nigra* 218
 Ruddy Duck *Oxyura jamaicensis* 35, 85, 96, 98, 147, 252, 329
 Hooded Merganser *Lophodytes cucullatus* 96, 117, 124, 126, 132, 147, 212, 265
 Common Merganser *Mergus merganser* 8, 96, 98, 126, 147, 290, 291
 Red-breasted Merganser *Mergus serrator* 198

ORDER FALCONIFORMES

Family Cathartidae

- ³ California Condor *Gymnogyps californianus* 259, 261
 Turkey Vulture *Cathartes aura* 18, 84, 98, 132, 147, 157, 165, 235, 237, 252, 261, 361

Family Accipitridae

- White-tailed Kite *Elanus leucurus* 237
 Goshawk *Accipiter gentilis* 98, 147, 293, 294
 Sharp-shinned Hawk *Accipiter striatus* 64a, 98, 147, 252
 Cooper's Hawk *Accipiter cooperii* 98, 132, 147, 252, 289, 293
 Red-tailed Hawk *Buteo jamaicensis* 18, 76a, 98, 127, 132, 147, 157, 165, 252, 293
⁴ Harlan's Hawk *Buteo harlani* 278
 Swainson's Hawk *Buteo swainsoni* 35, 98, 147, 165, 241, 252
 Rough-legged Hawk *Buteo lagopus* 182
 Ferruginous Hawk *Buteo regalis* 35, 98, 165, 241, 252
 Golden Eagle *Aquila chrysaetos* 98, 120, 147, 165, 237, 241, 252, 361
 Bald Eagle *Haliaeetus leucocephalus* 8, 83, 98, 111, 147, 235, 237, 241, 252, 261, 290, 291
 Marsh Hawk *Circus cyaneus* 98, 147, 165, 252, 285

Family Pandionidae

- Osprey *Pandion haliaetus* 8, 98, 121, 147, 241, 290, 291

Family Falconidae

- Gyr Falcon *Falco rusticolus* 278
 Prairie Falcon *Falco mexicanus* 8, 35, 64a, 98, 147, 163, 165, 241, 252, 261
 Peregrine Falcon *Falco peregrinus* 7, 8, 34, 98, 147, 241, 269
 Pigeon Hawk *Falco columbarius* 98, 105, 147, 241, 252
 Sparrow Hawk *Falco sparverius* 33, 35, 64a, 98, 132, 147, 157, 165, 252, 261, 293

³ Not cited in Bertrand and Scott (1971)—extirpated in Oregon.

⁴ Not cited in Bertrand and Scott (1971)—questionable identification.

ORDER GALLIFORMES

Family Tetraonidae

- Blue Grouse *Dendragapus obscurus* 98, 132, 147, 157, 241, 249, 252, 262, 330
- Spruce Grouse *Canachites canadensis* 157, 241, 249
- Ruffed Grouse *Bonasa umbellus* 17, 98, 132, 147, 157, 221, 249
- White-tailed Ptarmigan *Lagopus leucurus**
- Sharp-tailed Grouse *Pedioecetes phasianellus* 67, 159, 241, 249
- Sage Grouse *Centrocercus urophasianus* 14, 67, 157, 165, 249, 252

Family Phasianidae

- Bobwhite *Colinus virginianus* 15, 80, 81, 84, 132, 147, 249
- California Quail *Lophortyx californicus* 76a, 81, 147, 175, 243, 249
- Mountain Quail *Oreortyx pictus* 81, 98, 132, 147, 154, 249
- Ring-necked Pheasant *Phasianus colchicus* 18, 64a, 79, 80, 84, 112, 132, 147, 157, 165, 221, 247, 249, 342
- Chukar *Alectoris graeca* 249, 294
- Gray Partridge *Perdix perdix* 64a, 80, 147, 249
- Turkey *Meleagris gallopavo* 84, 147, 249

ORDER GRUIFORMES

Family Gruidae

- Sandhill Crane *Grus canadensis* 64a, 98, 141, 145, 147, 157, 165, 195, 241, 252, 290, 294, 325, 338

Family Rallidae

- Virginia Rail *Rallus limicola* 96, 132, 147, 165
- Sora *Porzana carolina* 96, 132, 147
- Yellow Rail *Coturnicops noveboracensis* 122, 241, 278
- American Coot *Fulica americana* 34, 85, 96, 132, 147, 165, 252, 261, 324, 329

ORDER CHARADRIIFORMES

Family Haematopodidae

- Black Oystercatcher *Haematopus bachmani**

Family Charadriidae

- Semipalmated Plover *Charadrius semipalmatus* 147, 234, 294
- Snowy Plover *Charadrius alexandrinus* 241
- Killdeer *Charadrius vociferus* 35, 64a, 96, 98, 132, 147, 165, 252
- Mountain Plover *Eypoda montana**
- American Golden Plover *Pluvialis dominica* 175, 234
- Black-bellied Plover *Squatarola squatarola* 147, 175, 240
- Surfbird *Aphriza virgata**
- Ruddy Turnstone *Arenaria interpres**
- Black Turnstone *Arenaria melanocephala**

Family Scolopacidae

- Common Snipe *Capella gallinago* 96, 147, 165, 252
- Long-billed Curlew *Numenius americanus* 64a, 147, 165
- Whimbrel *Numenius phaeopus* 147
- Upland Plover *Bartramia longicauda* 241
- Spotted Sandpiper *Actitis macularia* 35, 54, 64a, 98, 132, 147, 165, 252, 301
- Solitary Sandpiper *Tringa solitaria* 48, 96, 98, 147
- Wandering Tattler *Heteroscelus incanum* 98
- Willet *Catoptrophorus semipalmatus* 165, 252
- Greater Yellowlegs *Totanus melanoleucus* 96, 147, 327
- Lesser Yellowlegs *Totanus flavipes* 147
- Knot *Calidris canutus* 277
- Rock Sandpiper *Erolia philocephalus**
- Sharp-tailed Sandpiper *Erolia acuminata**
- Pectoral Sandpiper *Erolia melanotos* 48, 147
- Baird's Sandpiper *Erolia bairdii* 147, 363
- Least Sandpiper *Erolia minutilla* 147
- Dunlin *Erolia alpina* 96, 147, 335
- Short-billed Dowitcher *Limnodromus griseus* 96, 147, 175, 241
- Long-billed Dowitcher *Limnodromus scolopaceus* 96, 165
- Stilt Sandpiper *Micropalama himantopus**
- Semipalmated Sandpiper *Ereunetes pusillus**
- Western Sandpiper *Ereunetes mauri* 147
- Buff-breasted Sandpiper *Tryngites subruficollis**
- Marbled Godwit *Limosa fedoa* 39, 240
- Sanderling *Crocethia alba* 234

- Family Recurvirostridae
 American Avocet *Recurvirostra americana* 157, 165, 170, 350
 Black-necked Stilt *Himantopus mexicanus* 157, 241
- Family Phalaropodidae
 Red Phalarope *Phalaropus fulicarius* 7, 47, 78, 104, 162, 233, 313, 363
 Wilson's Phalarope *Steganopus tricolor* 98, 147, 157, 165, 170, 233, 252
 Northern Phalarope *Lobipes lobatus* 78, 96, 147, 233
- Family Stercorariidae
 Pomarine Jaeger *Stercorarius pomarinus* 363
 Parasitic Jaeger *Stercorarius parasiticus* 363
 Long-tailed Jaeger *Stercorarius longicaudus* 175, 301, 363
 Skua *Catharacta skua* 363
- Family Laridae
 Glaucous Gull *Larus hyperboreus* 147, 207, 301
 Glaucous-winged Gull *Larus glaucescens* 147, 273, 298, 301, 358
 Western Gull *Larus occidentalis* 100, 101, 147, 302, 303, 304, 307, 335, 358
 Herring Gull *Larus argentatus* 298, 301
 California Gull *Larus californicus* 8, 35, 98, 110, 147, 165, 252, 304, 358
 Ring-billed Gull *Larus delawarensis* 8, 42, 98, 147, 165, 252, 320
 Mew Gull *Larus canus**
 Franklin's Gull *Larus pipixcan* 48, 190, 241
 Bonaparte's Gull *Larus philadelphia* 147
 Heerman's Gull *Larus heermanni**
 Black-legged Kittiwake *Rissa tridactyla* 168, 301
 Red-legged Kittiwake *Rissa brevirostris* 267, 349
 Sabine's Gull *Xema sabini* 298, 363
 Forster's Tern *Sterna forsteri* 35, 98, 147, 157, 165, 171, 252
 Common Tern *Sterna hirundo* 35, 294, 352
 Arctic Tern *Sterna paradisaea* 171
 Least Tern *Sterna albifrons**
 Caspian Tern *Hydroprogne caspia* 35, 147, 241
 Black Tern *Chlidonias niger* 64a, 77, 96, 147, 157, 165, 252
- Family Alcidae
 Common Murre *Uria aalge* 34, 333, 341
 Thick-billed Murre *Uria lomvia**
 Pigeon Guillemot *Cepphus columba* 332, 333
 Marbled Murrelet *Brachyramphus marmoratus* 25, 241
 Xantus' Murrelet *Endomychura hypoleuca**
 Ancient Murrelet *Synthliboramphus antiquum* 192, 268
 Cassin's Auklet *Ptychoramphus aleutica* 34, 51, 189, 340
 Parakeet Auklet *Cyclorhynchus psittacula**
 Rhinoceros Auklet *Cerorhinca monocerata* 51, 241
 Horned Puffin *Fratercula corniculata* 135
 Tufted Puffin *Lunda cirrhata* 100
- ORDER COLUMBIFORMES
- Family Columbidae
 Band-tailed Pigeon *Columba fasciata* 18, 98, 147, 173, 249, 293, 312, 317, 331, 357
 Rock Dove *Columba livia* 98, 232, 289, 361
 Mourning Dove *Zenaidura macroura* 16, 37, 42, 76a, 98, 132, 147, 157, 165, 249, 252, 315, 328
- ORDER CUCULIFORMES
- Family Cuculidae
 Yellow-billed Cuckoo *Coccyzus americanus* 20, 147, 241, 282
- ORDER STRIGIFORMES
- Family Tytonidae
 Barn Owl *Tyto alba* 132, 147, 247
- Family Strigidae
 Screech Owl *Otus asio* 98, 132, 147, 174, 241, 261
 Flammulated Owl *Otus flammeolus* 241, 294
 Great Horned Owl *Bubo virginianus* 18, 43, 64a, 76a, 98, 125, 127, 132, 147, 165, 226, 244, 246, 247, 252
 Snowy Owl *Nyctea scandiaca* 147, 318, 319
 Pygmy Owl *Glaucidium gnoma* 98, 106, 132, 147, 241
 Burrowing Owl *Speotyto cunicularia* 35, 64a, 114, 143, 147, 157, 165, 177, 241
 Spotted Owl *Strix occidentalis* 69, 98, 132, 147, 241, 245
 Great Gray Owl *Strix nebulosa* 5, 127, 147, 155, 191, 241

Long-eared Owl *Asio otus* 35, 98, 147, 210, 244, 247, 248, 287
Short-eared Owl *Asio flammeus* 64a, 147, 165
Boreal Owl *Aegolius funereus**
Saw-whet Owl *Aegolius acadicus* 102, 147, 227

ORDER CAPRIMULGIFORMES

Family Caprimulgidae

Poor-will *Phalaenoptilus nuttallii* 98, 157, 165, 187, 241, 252
Common Nighthawk *Chordeiles minor* 76a, 98, 132, 147, 252, 308, 363

ORDER APODIFORMES

Family Apodidae

Black Swift *Cypseloides niger* 74, 147, 278
Vaux's Swift *Chaetura vauxi* 98, 131, 147, 165, 252
White-throated Swift *Aeronautes saxatalis* 98, 295

Family Trochilidae

Black-chinned Hummingbird *Archilochus alexandri* 21
Anna's Hummingbird *Calypte anna* 47, 49
Broad-tailed Hummingbird *Selasphorus platycercus**
Rufous Hummingbird *Selasphorus rufus* 8, 49, 98, 132, 147, 165, 179, 252
Allen's Hummingbird *Selasphorus sasin* 47, 241
Calliope Hummingbird *Stellula calliope* 35, 98, 179, 252

ORDER CORACIIFORMES

Family Alcedinidae

Belted Kingfisher *Megasceryle alcyon* 98, 132, 147, 165, 252, 290, 291

ORDER PICIFORMES

Family Picidae

Yellow-shafted Flicker *Colaptes auratus* 47, 50, 76a
Red-shafted Flicker *Colaptes cafer* 8, 18, 64a, 76a, 98, 129, 132, 147, 157, 165, 243, 252, 285, 289, 311
Hybrid Flicker *Colaptes cafer* X *auratus* 47, 147
Pileated Woodpecker *Dryocopus pileatus* 18, 98, 132, 147, 252
Acorn Woodpecker *Melanerpes formicivorus* 147, 157, 197, 201, 344, 354
Lewis' Woodpecker *Asyndesmus lewis* 32, 76a, 98, 132, 147, 241, 252
Yellow-bellied Sapsucker *Sphyrapicus varius* 18, 98, 132, 147, 165, 252
Williamson's Sapsucker *Sphyrapicus thyroideus* 76a, 98, 147, 252
Hairy Woodpecker *Dendrocopos villosus* 8, 18, 76a, 98, 132, 147, 157, 165, 252
Downy Woodpecker *Dendrocopos pubescens* 18, 55, 76a, 98, 132, 147, 165, 294
Nuttall's Woodpecker *Dendrocopos nuttallii* 310
White-headed Woodpecker *Dendrocopos albobarvatus* 36, 76a, 98, 252
Black-backed Three-toed Woodpecker *Picoides arcticus* 35, 98, 252
Northern Three-toed Woodpecker *Picoides tridactylus* 35, 98, 241

ORDER PASSERIFORMES

Family Tyrannidae

Eastern Kingbird *Tyrannus tyrannus* 35, 157, 165, 252
Tropical Kingbird *Tyrannus melancholicus**
Western Kingbird *Tyrannus verticalis* 114, 142, 147, 157, 165, 211, 252, 285
Cassin's Kingbird *Tyrannus vociferans* 175
Scissor-tailed Flycatcher *Muscivora forficata**
Ash-throated Flycatcher *Myiarchus cinerascens* 147, 154, 279
Eastern Phoebe *Sayornis phoebe* 241
Black Phoebe *Sayornis nigricans* 95, 175, 241, 288
Say's Phoebe *Sayornis saya* 76a, 98, 147, 165, 252
Traill's Flycatcher *Empidonax traillii* 35, 98, 132, 147, 252, 271, 274
Hammond's Flycatcher *Empidonax hammondi* 35, 98, 124, 147, 186, 202, 203, 204, 206, 252
Dusky Flycatcher *Empidonax oberholseri* 98, 124, 147, 165, 202, 205, 252
Gray Flycatcher *Empidonax wrightii* 76a, 165, 202, 205
Western Flycatcher *Empidonax difficilis* 35, 45, 98, 132, 147, 252, 301
Western Wood Pewee *Contopus sordidulus* 18, 76a, 98, 132, 147, 165, 252
Olive-sided Flycatcher *Nuttallornis borealis* 35, 98, 124, 132, 147, 252

Family Alaudidae

Horned Lark *Eremophila alpestris* 26, 35, 98, 132, 147, 165, 176, 346

Family Hirundinidae

Violet-green Swallow *Tachycineta thalassina* 62, 63, 64a, 98, 132, 139, 147, 165, 252, 289
Tree Swallow *Iridoprocne bicolor* 98, 132, 139, 147, 165, 240, 252, 285, 289

- Bank Swallow *Riparia riparia* 147, 165
 Rough-winged Swallow *Stelgidopteryx ruficollis* 98, 132, 147, 165
 Barn Swallow *Hirundo rustica* 91, 97, 98, 132, 143, 147, 165, 252, 285
 Cliff Swallow *Petrochelidon pyrrhonota* 64a, 98, 132, 147, 165, 252, 285
 Purple Martin *Progne subis* 2, 147, 241, 289
- Family Corvidae
 Gray Jay *Perisoreus canadensis* 3, 11, 98, 124, 132, 147, 157, 234, 252
 Steller's Jay *Cyanocitta stelleri* 3, 6, 18, 76a, 98, 132, 147, 157, 252
 Scrub Jay *Abelocoma coerulescens* 18, 98, 132, 147, 157, 241, 243, 275, 276
 Black-billed Magpie *Pica pica* 35, 59, 64a, 76a, 98, 147, 150, 157, 165, 232, 252, 261, 361
 Common Raven *Corvus corax* 64a, 76a, 85, 98, 147, 157, 165, 235, 252, 261
 Common Crow *Corvus brachyrhynchos* 42, 84, 98, 132, 147, 157, 161, 165, 232, 235, 261
 Northwestern Crow *Corvus caurinus**
 Piñon Jay *Gymnorhinus cyanocephalus* 44, 72, 76a, 157
 Clark's Nutcracker *Nucifraga columbiana* 35, 47, 76a, 98, 157, 252, 293
- Family Paridae
 Black-capped Chickadee *Parus atricapillus* 18, 28, 52, 75, 76a, 132, 147, 154, 165
 Mountain Chickadee *Parus gambeli* 76a, 98, 130, 252
 Chestnut-backed Chickadee *Parus rufescens* 98, 132, 147
 Plain Titmouse *Parus inornatus* 157, 167, 241
 Common Bushtit *Psaltiriparus minimus* 4, 18, 98, 132, 147, 294
- Family Sittidae
 White-breasted Nuthatch *Sitta carolinensis* 12, 18, 76a, 98, 132, 139, 147, 153, 252
 Red-breasted Nuthatch *Sitta canadensis* 3, 8, 18, 54, 76a, 98, 132, 147, 252
 Pygmy Nuthatch *Sitta pygmaea* 76a, 98, 240, 252, 270
- Family Certhiidae
 Brown Creeper *Certhia familiaris* 14, 18, 98, 132, 147, 252
- Family Chamaeidae
 Wrentit *Chamaea fasciata* 143, 147, 157
- Family Cinclidae
 Dipper *Cinclus mexicanus* 35, 98, 132, 147
- Family Troglodytidae
 House Wren *Troglodytes aedon* 76a, 98, 132, 139, 147, 165, 252, 289
 Winter Wren *Troglodytes troglodytes* 18, 53, 76a, 93, 98, 132, 147
 Bewick's Wren *Thryomanes bewickii* 18, 98, 132, 147, 241
 Long-billed Marsh Wren *Telmatodytes palustris* 14, 92, 132, 147, 149, 165
 Cañon Wren *Catherpes mexicanus* 14, 136, 165, 252, 294
 Rock Wren *Salpinctes obsoletus* 35, 98, 147, 165, 252
- Family Mimidae
 Mockingbird *Mimus polyglottos* 99, 158, 166, 241, 321, 349
 Catbird *Dumetella carolinensis* 14, 35, 159, 241, 326
 Brown Thrasher *Toxostoma rufum* 20, 240
 California Thrasher *Toxostoma redivivum**
 LeConte's Thrasher *Toxostoma lecontei**
 Sage Thrasher *Oreoscoptes montanus* 35, 64a, 76a, 157, 252
- Family Turdidae
 Robin *Turdus migratorius* 18, 64a, 76a, 98, 118, 132, 147, 165, 193, 243, 252, 293, 331
 Varied Thrush *Ixoreus naevius* 3, 18, 76a, 98, 132, 147, 169, 243, 286, 298
 Hermit Thrush *Hylocichla guttata* 35, 76a, 98, 147, 157, 165, 252
 Swainson's Thrush *Hylocichla ustulata* 35, 98, 132, 147
 Veery *Hylocichla fuscescens* 9, 165, 241
 Western Bluebird *Sialia mexicana* 18, 76a, 98, 132, 147, 154, 241, 289, 294
 Mountain Bluebird *Sialia currucoides* 8, 64a, 76a, 98, 147, 165, 252
 Townsend's Solitaire *Myadestes townsendi* 18, 35, 64a, 76a, 98, 147, 157, 252, 294, 347
- Family Sylviidae
 Blue-gray Gnatcatcher *Poliophtila caerulea* 147, 241, 280, 288
 Golden-crowned Kinglet *Regulus satrapa* 18, 76a, 98, 124, 132, 147, 252
 Ruby-crowned Kinglet *Regulus calendula* 18, 35, 52, 76a, 98, 147, 252, 331
- Family Motacillidae
 Water Pipit *Anthus spinoletta* 98, 147, 157, 241, 252
- Family Bombycillidae
 Bohemian Waxwing *Bombycilla garrulus* 128, 147, 241
 Cedar Waxwing *Bombycilla cedrorum* 18, 56, 76a, 98, 132, 147
- Family Prilognatidae
 Phainopepla *Phainopepla nitens* 48, 240

Family Laniidae

- Northern Shrike *Lanius excubitor* 57, 147
Loggerhead Shrike *Lanius ludovicianus* 64a, 165, 252, 314

Family Sturnidae

- Starling *Sturnus vulgaris* 147, 184, 225, 231, 243, 247, 283, 284, 285, 294, 348
Crested Myna *Acridotheres cristatellus**

Family Vireonidae

- Bell's Vireo *Vireo bellii**
Hutton's Vireo *Vireo huttoni* 18, 147, 241
Solitary Vireo *Vireo solitarius* 18, 98, 132, 147, 214, 252
Red-eyed Vireo *Vireo olivaceus* 35, 47, 54, 76a, 132, 233, 234, 253
Warbling Vireo *Vireo gilvus* 18, 98, 147, 252

Family Parulidae

- Black and White Warbler *Mniotilta varia* 234
Blue-winged Warbler *Vermivora pinus**
Tennessee Warbler *Vermivora peregrina* 233
Orange-crowned Warbler *Vermivora celata* 18, 35, 98, 132, 140, 147, 165, 185, 252
Nashville Warbler *Vermivora ruficapilla* 35, 98, 132, 147
Parula Warbler *Parula americana**
Yellow Warbler *Dendroica petechia* 18, 35, 98, 132, 147, 165, 252
Cape May Warbler *Dendroica tigrina**
Black-throated Blue Warbler *Dendroica caerulescens* 233, 234, 240
Myrtle Warbler *Dendroica coronata* 147
Audubon's Warbler *Dendroica auduboni* 18, 35, 76a, 98, 132, 147, 156, 159, 165, 252
Black-throated Gray Warbler *Dendroica nigrescens* 18, 96, 132, 147, 252
Townsend's Warbler *Dendroica townsendi* 35, 52, 71, 76a, 98, 147, 178, 252
Hermit Warbler *Dendroica occidentalis* 98, 147, 178
Chestnut-sided Warbler *Dendroica pennsylvanica**
Bay-breasted Warbler *Dendroica castanea* 253
Blackpoll Warbler *Dendroica striata**
Palm Warbler *Dendroica palmarum**
Ovenbird *Seiurus aurocapillus* 233
Northern Waterthrush *Seiurus noveboracensis* 233
MacGillivray's Warbler *Oporornis tolmiei* 18, 98, 132, 147, 165, 252
Yellowthroat *Geothlypis trichas* 27, 29, 132, 147, 165, 252, 285
Yellow-breasted Chat *Icteria virens* 35, 62, 132, 147, 165
Wilson's Warbler *Wilsonia pusilla* 18, 52, 98, 116, 132, 147, 165, 181, 238, 252
American Redstart *Setophaga ruticilla* 35, 233, 234, 241, 281, 282

Family Ploceidae

- House Sparrow *Passer domesticus* 98, 132, 139, 147, 165, 243, 252, 289, 293

Family Icteridae

- Bobolink *Dolichonyx oryzivorus* 165, 241
Western Meadowlark *Sturnella neglecta* 35, 76a, 98, 132, 147, 157, 165, 252
Yellow-headed Blackbird *Xanthocephalus xanthocephalus* 64a, 87, 146, 147, 157, 165, 213, 252, 329
Red-winged Blackbird *Agelaius phoeniceus* 4, 88, 94, 98, 132, 147, 165, 243, 252, 285, 348, 351
Tricolored Blackbird *Agelaius tricolor* 241, 288
Hooded Oriole *Icterus cucullatus* 48
Baltimore Oriole *Icterus galbula* 234
Bullock's Oriole *Icterus bullockii* 132, 147, 165, 252, 353
Rusty Blackbird *Euphagus carolinus* 351
Brewer's Blackbird *Euphagus cyanocephalus* 64a, 76a, 88, 98, 132, 147, 150, 157, 165, 243, 252, 285, 293, 348, 351
Brown-headed Cowbird *Molothrus ater* 4, 18, 98, 138, 147, 165, 201, 214, 243, 300, 339

Family Thraupidae

- Western Tanager *Piranga ludoviciana* 18, 76a, 98, 132, 147, 165, 252

Family Fringillidae

- ⁵ Cardinal *Richmondia cardinalis* 188
Black-headed Grosbeak *Phencticus melanocephalus* 35, 62, 98, 132, 147, 165
Lazuli Bunting *Passerina amoena* 18, 98, 132, 147, 165
Painted Bunting *Passerina ciris* 233
Indigo Bunting *Passerina cyanea**
Brambling *Fringilla montifringilla* 22
Dickcissel *Spiza americana* 351
Evening Grosbeak *Hesperiphona vespertina* 35, 76a, 98, 147, 252
Purple Finch *Carpodacus purpureus* 76, 76a, 98, 132, 147, 165, 233, 252

⁵ Not cited in Bertrand and Scott (1971)—A probable release from captivity.

- Cassin's Finch *Carpodacus cassinii* 35, 76, 98
 House Finch *Carpodacus mexicanus* 4, 18, 22, 76a, 113, 119, 147, 157, 165, 172, 201, 236, 252, 293
 Pine Grosbeak *Pinicola enucleator* 35, 48, 76a, 98, 159, 241
 Gray-crowned Rosy Finch *Leucosticte tephrocotis* 8, 35, 98, 157, 241, 256
 Black Rosy Finch *Leucosticte atrata* 241
 Common Redpoll *Acanthis flammea* 147
 Pine Siskin *Spinus pinus* 14, 35, 76a, 98, 108, 147, 252
 American Goldfinch *Spinus tristis* 18, 98, 132, 147, 154, 165, 289, 293, 331, 343
 Lesser Goldfinch *Spinus psaltria* 132, 147
 Lawrence's Goldfinch *Spinus lawrencei**
 Red Crossbill *Loxia curvirostra* 8, 35, 98, 133, 137, 147, 157, 252
 White-winged Crossbill *Loxia leucoptera* 196, 255
 Green-tailed Towhee *Chlorura chlorura* 76a, 98, 157, 159, 252
 Rufous-sided Towhee *Pipilo erythrophthalmus* 3, 18, 76a, 98, 132, 147, 157, 243, 292, 331
 Brown Towhee *Pipilo fuscus* 68, 148
 Lark Bunting *Calamospiza melanocorys* 114
 Savannah Sparrow *Passerculus sandwichensis* 35, 64a, 98, 132, 147, 165, 252, 337
 Grasshopper Sparrow *Ammodramus savannarum* 241, 288
 Vesper Sparrow *Pooecetes gramineus* 132, 147, 165, 323
 Lark Sparrow *Chondestes grammacus* 98, 147, 165
 6 Rufous-crowned Sparrow *Aimophila ruficeps* 76a
 Black-throated Sparrow *Amphispiza bilineata* 46, 73, 158, 241
 Sage Sparrow *Amphispiza belli* 35, 165, 252, 263, 264
 Slate-colored Junco *Junco hyemalis* 147, 234
 Oregon Junco *Junco oregonus* 3, 18, 19, 64a, 76a, 98, 109, 123, 132, 147, 217, 243, 252, 258, 298, 306
 Tree Sparrow *Spizella arborea* 76a, 147, 159, 334
 Chipping Sparrow *Spizella passerina* 8, 18, 76a, 98, 132, 147, 165, 252
 Brewer's Sparrow *Spizella breweri* 35, 165, 252
 Black-chinned Sparrow *Spizella atrogularis**
 Harris' Sparrow *Zonotrichia querula* 229, 234, 240, 278, 288, 322, 349
 White-crowned Sparrow *Zonotrichia leucophrys* 3, 23, 24, 30, 31, 64, 76a, 98, 132, 147, 157, 165, 252, 298
 Golden-crowned Sparrow *Zonotrichia atricapilla* 3, 76a, 98, 147, 229, 243, 334
 White-throated Sparrow *Zonotrichia albicollis* 76a, 147, 228, 234, 240, 278, 360
 Fox Sparrow *Passerella iliaca* 10, 18, 23, 66, 76a, 98, 147, 165, 243, 252
 Lincoln's Sparrow *Melospiza lincolni* 52, 76a, 98, 147, 252, 257, 260
 Swamp Sparrow *Melospiza georgiana* 52
 Song Sparrow *Melospiza melodia* 4, 18, 35, 64a, 98, 132, 138, 147, 165, 208, 243, 252, 298
 Lapland Longspur *Calcarius lapponicus**
 Snow Bunting *Plectrophenax nivalis* 41

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Growth and Reproduction of Red Elderberry on Subalpine Rangeland in Utah

Red elderberry (*Sambucus racemosa* L. spp. *pubens* (Michx.) House var. *microbotrys* (Rydb.) Kearney and Peebles) is distributed chiefly from the southern Rocky Mountains, west to the Sierra Nevada, and north into southern Idaho (Hitchcock *et al.*, 1959). In Utah, it often occurs in high density stands throughout the subalpine zone in vegetation types ranging from aspen (*Populus tremuloides*) woodland to open herbland and brush vegetation (Fig. 1). The foliage is highly palatable to livestock, particularly in early fall when availability of other forage is reduced. The fruit, leaves, and stems provide food for big game, birds, and small mammals during the fall and winter months.

Some information about red elderberry is available on allelopathic effects (McDonough and Tew, 1967), germination (McDonough, 1969), and on injury by small mammals (Smith, 1965, 1969). The study reported here deals with ecological and physiological aspects relating to growth and reproduction of red elderberry.

Study Sites

The field portion of this study was conducted on the Mud Creek Sheep Allotment (Uinta National Forest) and in Tony Grove Canyon (Cache National Forest), both in northern Utah. Elevations are within the 2200-2500 m range. At Mud Creek, the surface soils range from loams to sandy clay loams composed of Uinta Formation materials (lacustrine sandstone, limestone, and shale), as described by Matthews (1965). At Tony Grove, the soils are predominantly loams and silt loams derived from components of the Wasatch Formation (conglomerate overlying limestone) and from glacial till (Sharif, 1967).

Red elderberry is widespread on both study sites. It occurs, at least sparingly, in the broad range of vegetation types and soil conditions found on these sites. However, there is a trend toward best development on deeper soils. The species grows beneath the overstory of aspen, the dominant vegetation on the study sites, but it is most abundant in openings within aspen stands. It is also found in scattered stands of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*); and with big sagebrush (*Artemisia tridentata*), snowberry (*Symphoricarpos oreophilus*), and other shrubs. The most important perennial herbs associated with red elderberry at Mud Creek are: slender wheatgrass (*Agropyron trachycaulum*), polyanthus brome (*Bromus polyanthus*), Wasatch bluegrass (*Poa curta*), and tall bluebells (*Mertensia*

¹ Stationed in Logan, Utah, at the Forestry Sciences Laboratory, maintained in cooperation with Utah State University.



Figure 1. Photograph of clones of red elderberry on open ground at Mud Creek.

arizonica var. *leonardi*); and at Tony Grove, polyanthus brome, butterweed groundsel (*Senecio serra*), and western coneflower (*Rudbeckia occidentalis*).

Average annual precipitation in these areas is about 75 cm and falls mostly as snow. Maximum snow accumulation, 2 to 3 m, takes place from November to April. Temperatures during the growing season generally range between 5° and 25°C. Frosts can occur during any month.

Methods

Growth measurements, clipping treatments, and observations of morphology, phenology, and reproduction were made between 1965 and 1970 on selected clones within live-stock exclosures at each of the two study sites. At Mud Creek, stem density was determined for five years (1966-1970) on 25 permanently marked 1.2- by 1.2-m quadrats on each of 11 areas, one-fifth hectare in size. The exclosures and marked areas were located in relatively dense stands of red elderberry.

Growth studies of both laboratory-germinated seedlings and transplants from the field were conducted in a greenhouse and in Sherer (Model CEL 37-14)² growth chambers. Transplants from the field, collected in the fall, consisted of 30-cm lengths of rhizomes with rhizome stems attached. These transplants were potted in native soil in 2.5-gal containers, and sets of containers were held either under greenhouse conditions or were moist-stratified for four months at 2°C before transfer of all containers to growth chambers. Controlled conditions tested for growth responses of plants in sets of four containers were: temperature alternations of 25/15°C or 15/5°C, with 12-hr high-intensity photoperiods (3500 ft-c) coinciding with the higher temperature of the alternation or with low-level supplementary illumination (100 ft-c) to give 18-hr photoperiods.

To determine viability and germinability of seed, ripe fruit clusters were collected in 1968 from five clones at each site and also from Ephraim Canyon (elevation, 2700 m), Manti LaSal National Forest in central Utah. The fruits were macerated in water and the empty seeds and debris separated out by flotation. Viability of the filled seed was tested with a 1 percent solution of 2,3,5-triphenyl-tetrazolium chloride. Laboratory germination tests were run at temperature alternations that ranged from 5° to 30°C and at a stratification temperature of 2°C in petri dish germinators as described by McDonough (1969). Germination was also checked after stratification under field conditions. Nylon bags containing sand-seed mixtures were placed on the soil surface at each study site prior to the first snow in late September 1968. Periodically, from December through May, a bag was recovered and seed germination observed. Emergence and survival of seedlings were also determined from field-planted seed.

Results

Growth

Large variations in the size of individual clones of the red elderberry were found and presumably reflect differences in age. Complete excavation of a large clone at Mud Creek showed that rhizomes and major roots extended to a depth of approximately 1 m over a 4- by 5-m area. Clone size, estimated from the extent of dye translocation in rhizomes and by pattern analysis of density data from belt transects (Greig-Smith, 1964), showed variation ranging from less than 1 m² to 16 m².

Rhizomes form buds, some of which emerge as rhizome stems by the time of snowmelt each year. These stems are strictly vegetative and remain unbranched during the first growing season (Fig. 2). Axillary buds are formed late in the growing season and some of these buds grow into either vegetative or flowering branches during the

²The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such does not constitute an official endorsement or approval by the U.S. Department of Agriculture of any product or service to the exclusion of others which may be suitable.

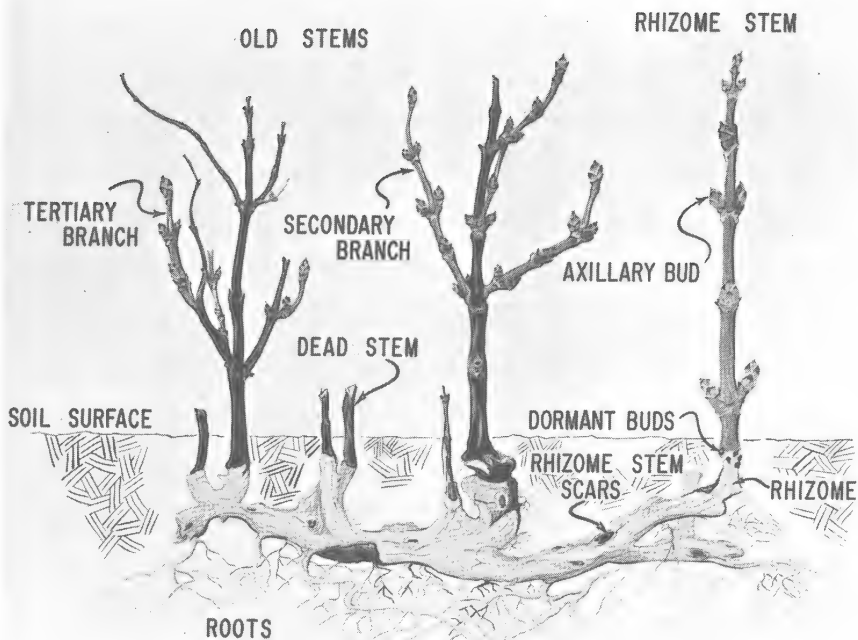


Figure 2. Sketch of red elderberry clone in winter condition.

following year. A few axillary buds at the unelongated, lower nodes of the rhizome stems remain dormant for one or more years.

Growth of axillary buds on one-year-old rhizome stems ("old stems") results in secondary branch development. Subsequent bud growth on these branches the third year results in tertiary branch development, etc. However, branches of tertiary order or higher are not commonly present in the field because of frost and/or animal damage to buds and stems over the winter. During five years (1966-1970) at Mud Creek, only 7 percent of an average of 2.8 branches per old stem were tertiary or higher order branches. Of 60 secondary branches measured and observed at Tony Grove in 1969, 40 percent produced flowers; the remaining branches were vegetative. On the average, the determinate flowering branches were 13 percent shorter than the vegetative branches on the same node. Both types of branches trended toward a reduction in total length when they originated at higher positions on the old stem. Average length, weight, and number of nodes and leaves for vegetative and flowering branches and rhizome stems at Mud Creek in 1968 and 1969 are presented in Table 1.

Bud expansion began under snow depths as great as 1/2 m. Stem growth of flowering branches was nearly completed within three to four weeks after snowmelt and that of vegetative branches and rhizome stems, within five to six weeks (Fig. 3). The date of flower initiation varied from mid-June to early July and coincided with a sharp reduction in the rate of vegetative growth. Fruit and seed maturation occurred between late July and mid-August after vegetative growth had ceased.

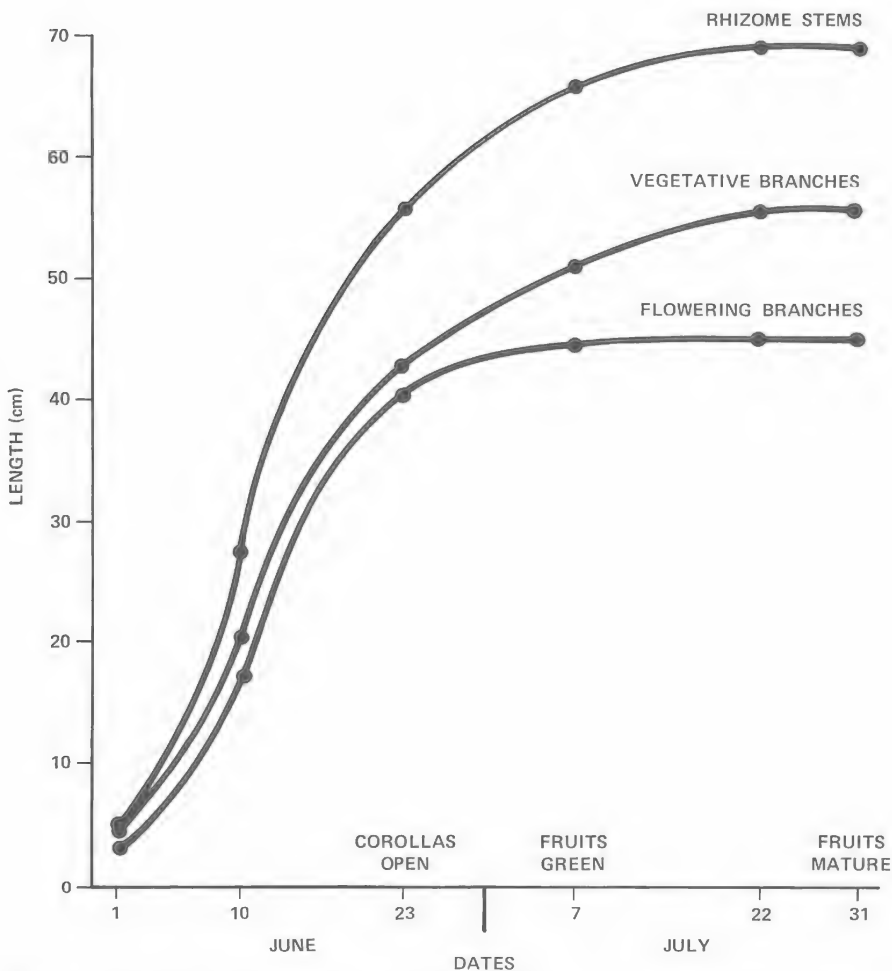


Figure 3. Growth and phenological development of red elderberry by date from 10 observations of each type among 10 clones, Tony Grove, 1968.

TABLE 1. Average length, weight, and number of nodes and leaves for vegetative and flowering branches and rhizome stems, Mud Creek, 1968-1969.

Type of growth ¹	Average length	Average Dry Weight			Average number	
		Stem tissue	Leaf tissue	Reproductive tissue ²	Nodes	Leaves
Rhizome stems	Centimeters 66	8.2	Grams 7.0	—	6	10
Vegetative branches	48	4.2	6.0	—	5	9
Flowering branches	37	1.3	3.1	0.8	3	6

¹ Six hundred rhizome stems, 210 vegetative branches, and 118 flowering branches were examined.

² Cymes bearing ripened fruit.

Growth of stems and branches under controlled conditions was best at temperature alternations of 25/15°C and 18-hr photoperiods following a stratification pretreatment. Other conditions—no stratification, temperature alternations of 15/5°C, and 12-hr photoperiods—gave inferior results. However, the best growth under controlled conditions was not more than 40 percent of that attained in the field. Possible reasons for this reduced growth include an insufficient supply of growth regulators or essential metabolites in the rhizome sections and stems, low illuminance compared to field conditions, or restricted soil volume in the containers.

Effects of Foliage Removal and Other Injury

In the event of injury to rhizome stems and branches by late-spring frosts or removal of all living above-ground parts by clipping, additional rhizome stems emerge within two to four weeks from a reserve of dormant rhizome buds. In an experiment in which all stems of four clones were clipped at ground level in mid-June of 1968, an average regrowth per clone of 136 percent of the original number of stems had occurred by the end of August. A second clipping at this time reduced the number of stems produced the following year to 37 percent of the original number. When branches were removed in mid-July from other clones, 18 percent of the original number of branches developed within two to four weeks—mainly from buds at the bases of the old stems. However, there were no rhizome stems initiated by this treatment. These experiments suggest that the suppressing effect of new growth over dormant buds is specific (*i.e.*, the presence of rhizome stems suppresses rhizome bud growth and the presence of branches suppresses bud growth on old stems).

In another experiment, clipping all stems of four clones to ground level at the end of each growing season (1963-1965) did not cause a significant difference in the number or in the length of rhizome stems produced in 1964, 1965, or 1966. The weight of stems and leaves did not change significantly either. When plants were enclosed in hardware cloth to protect them from rodent and snowpack damage in 1963, numerous branches, but few rhizome stems, were produced during the next two years. Even though the number of branches increased significantly, the length of branches was not significantly affected. During the third winter, nearly all old growth was killed by unusually severe weather conditions; consequently, numerous rhizome stems and few branches appeared the following summer.

Porcupines and mice feed on the buds and bark of red elderberry during the winter months. Porcupines work on top of the snow; mice, under and within the snowpack. Smith (1965) reported that red elderberry stems in 20 plots on Mud Creek had an average 21 percent of the bark removed from the stems during the winter of 1963-1964. The damage was primarily attributed to the long-tailed field mouse (*Microtus longicaudus*). *Microtus* population density peaked at that time.

As a result of various forms of injury (spring frosts, damage by rodents in winter, and snow damage), the density of old, living stems and, consequently, the density of branches varied considerably during the study (Table 2). The density of rhizome stems was considerably more stable than that of old, living stems, and the densities of the two groups were negatively correlated ($r = -0.87$). The density of total living stems varied little from year to year, as indicated by the coefficients of variation in Table 2.

From 1967, highest density year, to 1969, next to the lowest year for density,

TABLE 2. Average density per hectare of red elderberry stems on 25 permanently marked 1.2-by 1.2-m quadrats from 11 one-fifth hectare areas, Mud Creek Sheep Allotment, 1966-1970.

Year	Living stems			Old dead stems ¹
	Rhizome	Old	Total	
1966	54,040	6,630	60,670	—
1967	43,370	19,330	62,700	41,340
1968	48,120	4,970	53,090	57,730
1969	52,350	1,170	53,520	51,920
1970	41,690	18,150	59,840	35,370
$\bar{x}$	47,910	210,050	57,960	46,590
C.V. (%)	11	81	8	22

¹ Old dead stems = total live stems (the previous year) minus old living stems.

² From 1966 to 1970, old stems produced an average of 28,490 branches.

total live-stem density decreased 15 percent. However, during the same period, the ratio of rhizome stems to old stems increased over 20 times. In 1969, this large increase in ratio was caused primarily by two nights of freezing temperatures the previous year (late June 1968) that killed or injured all current growth of red elderberry plants. Within two weeks after the frost, numerous rhizome stems were initiated from dormant rhizome buds. These stems, which were initiated in late spring, and the injured rhizome stems and branches grew to less than one-half normal length that season. Axillary bud development was severely impaired by this setback and few branches developed in 1969. However, rhizome bud development was not impaired, since the number of rhizome stems was high in 1969 (Table 2).

The density of old dead stems is the total of all stems that died (total mortality) during the previous winter and early growing season. Mortality over five years averaged 46,590 stems per hectare, which is close to the 47,910 rhizome stems initiated each year.

Production and Utilization

At Mud Creek, red elderberry produced an average of just under 1000 kg of vegetative matter per hectare per year. Of this amount, 50 percent was stem tissue, 49 percent was leaf tissue, and 1 percent was reproductive tissue (Table 3). Livestock do not

TABLE 3. Average annual production (kilograms per hectare) of red elderberry at Mud Creek calculated from average weights (Table 1) and average densities (Table 2).

Type of tissue	Rhizome stems	Vegetative branches ¹	Flowering branches ¹	Total	Percent of total tissue
Stem	393	72	15	kg/ha 480	50
Leaf	335	103	35	473	49
Reproductive	—	—	9	9	1
Total				962	100

¹ Based on division of average branch density, 60 percent vegetative branches and 40 percent flowering branches.

normally eat this species until late August or early September unless other forage is scarce. Sheep at Mud Creek utilized 80 to 90 percent of the leaves (34 to 38 percent of total production) during most years, leaving only petioles and leaves that were out

of reach. At Tony Grove, cattle utilized 40 to 70 percent of the leaves and some stem tissue. At times, deer make considerable use of red elderberry leaves in late summer and early fall.³ Smith (1953) reported that captive deer in summer feeding trials (May through September) had an average preference index of 9 for red elderberry; the preference index for other browse species ranged from 5 to 32. Red elderberry was not fed to animals before June 21 or after August 22.

Reproduction by Seed

Fruits are produced by 60 to 90 percent of the 100 to 400 flowers in each inflorescence; the remainder of the flowers abscise or the fruits abort. Individual fruits contain two to four seeds (an average of 3.1). Flotation of seeds on water showed that on an average 39 percent were not completely filled or were empty. Light seeds were not confined to fruits of particular plants or sites, but were found in all but one of the fruit clusters examined. Filled seed gave 74 to 91 percent positive viability tests (Table 4).

TABLE 4. Average percent germination and viability of filled elderberry seeds from three sites in Utah, 1968.

Site	Percent germination ¹		Percent viability ²
	At 2°C	After transfer to 25/15°C	
Mud Creek	35 ¹ a	4 ^c	83
Tony Grove	50 ^a	7 ^c	91
Ephraim Canyon	37 ^b	4 ^c	74

¹ Based on three trials, 50 seeds per trial.

² Based on examination of 100 seeds after treatment with 2,3,5-triphenyl-tetrazolium chloride.

³ Percentages with the same superscript do not differ significantly at the 5 percent level as determined by variance analysis and Studentized range tests (Goldstein, 1964).

Seeds failed to germinate during 30 days incubation at alternating temperatures of 30/20, 25/15, or 15/5°C (8 hr light/16 hr dark). Stratification for five months at 2°C resulted in germination percentages of 37 to 51 percent, and an additional 4 to 7 percent upon return to a higher incubation temperature of 25/15°C (Table 4). The germination percentages were significantly lower for the seeds from Ephraim Canyon. McDonough (1969) reported that no germination was obtained from seeds stratified at 2°C for three months.

Following germination, seedlings grew normally under greenhouse conditions. Beyond the cotyledonary stage, four to six simple leaves were formed, then two to six trifoliate leaves, followed by the five to seven foliate adult leaves. By the third year, seedlings had produced a thickened crown bearing buds that had a potential for growth as rhizomes.

Germination and emergence in the field was poor. Seeds stratified in the field during fall and winter began germinating in March, and 8 percent (maximum) had germinated by early April. This field germination was low compared to laboratory results (Table 4) and may have been due to the freezing of the seed before a permanent snow cover developed. However, natural seeding would be subject to the same conditions. Emergence of seedlings from 1200 fall-planted seeds under aspen at the Tony Grove site amounted to one-half of 1 percent; none of the emergent seedlings sur-

³ Julander, Odell. Intermountain Forest and Range Experiment Station, Ogden, Utah. Personal communication.

vived the summer. Established seedlings were rarely observed in the field over a five-year period at Mud Creek and a three-year period at Tony Grove. The single exception occurred in an area where logging slash had been burned at Mud Creek; in this area seedlings were abundant.

Discussion

The persistence and spread of red elderberry on subalpine rangeland depends on vegetative reproduction rather than reproduction by seed. A tremendous vegetative reproductive potential was demonstrated repeatedly during the study by natural occurrences and clipping experiments. Field observations showed reproduction by seed was virtually nonexistent.

The debarking of stems and removal of buds by rodents and severe climatic conditions cause extreme fluctuations in the density of branches. This type of damage does not seem to be detrimental to the species, even though fruit production is almost eliminated in years when branch density is low. In terms of the persistence of the species, however, because reproduction by seed is minimal, the failure to fruit is not significant. Since livestock and game seldom utilize red elderberry until late in the growing season (and then eat the leaves primarily), it is doubtful that grazing will ever constitute a serious threat to the persistence of this species.

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Comparative Limnology and Phytoplankton Ecology of Four "Oligotrophic" Lakes in Oregon, U.S.A., with Emphasis on Lake Typology¹

Introduction

Lakes which are classified as oligotrophic possess, in theory, the attributes summarized by Welch (1952). Oligotrophy implies, basically, that lake biological production is restricted by a relatively poor supply of dissolved nutrients. But production and biomass will likely vary among lakes—from extremes of ultra-oligotrophy to conditions bordering vaguely on eutrophy. Some workers (*e.g.*, Naumann, 1932; Brundin, 1958; Jarnefelt, 1958) have defined various grades of oligotrophy; but these interpretations are often disputed, and may not apply universally.

The literature indicates that at least four lakes in Oregon are classified as "oligotrophic"—Crater (Donaldson, 1968), Odell (Newcomb, 1941; Averett, 1966), Waldo (Carter *et al.*, 1966) and Woahink (Gahler, 1969). In comparing these lakes, considerable differences were noted concerning basin origin, surface elevation, watershed features, morphometry, optical and chemical properties, and how the lakes were being used. Despite the diversity, however, each lake featured many limnological properties (Welch, 1952; Ruttner, 1953) that denoted oligotrophy.

This study evaluates the classification "oligotrophic" as applied to the four lakes. It considers the various edaphic, morphometric, climatic, and cultural factors that acted upon the lake environments and discusses the difficulty of classifying lakes using the familiar oligotrophic-mesotrophic-eutrophic categories. Specific objectives were to document, further, the limnology of these unusual lakes and to determine the extent to which biological production and biomass—particularly with regard to the phytoplankton—might differ among them.

The Lakes

Relative locations, sizes, and shapes of the four study lakes are illustrated in Figures 1 and 2. Lake morphometry and climate are summarized in Tables 1 and 2, respectively. A description of the lake basins follows.

Crater Lake

Crater Lake is the deepest lake in the United States and the seventh deepest in the world. The lake is located in the southwestern quarter of Oregon, approximately 105 km north of the Oregon-California border, and 195 km inland from the Pacific Ocean (Fig. 1).

¹ This study was funded by the U.S. Department of Interior, Office of Water Resources Grant No. 14-31-0001-3067, and was part of a thesis submitted for the Ph.D. degree at Oregon State University, Corvallis.



Figure 1. Locations of study lakes in Oregon.

TABLE 1. Morphometry of study lakes, Oregon.

	Crater ¹	Odell	Waldo	Woahink ²
Elevation, surface (m)	1882	1459	1650	12
Area (km ²)	48.0	14.4	25.1	3.2
Volume (km ³)	16.0	0.59	0.95	0.04
Depth, maximum (m)	589	86	128	21
Depth, mean (m)	325	41	38	10.5
Shoreline length (km)	31.0	21.5	40.0	22.3
Shoreline development	1.27	1.59	2.25	3.50
Relative depth (%)	7.52	2.01	2.26	1.18
Mean depth: max depth	0.55	0.48	0.30	0.50
Max depth: surface	0.085	0.023	0.026	0.012

¹Byrne (1965).

²McGie and Breuser (1962).

TABLE 2. Air temperature and precipitation averages of study lake basins, Oregon.¹

	Crater	Odell	Waldo ²	Woahink
Annual mean temperature (° C)	3.5	5.0		11.2
Annual mean precipitation (cm)	177.8	152.4		217.2

¹Data from 10-year (1951-1960) climatic summary of the United States (U.S. Weather Bureau, 1965).

²Nearest recording station located at Odell Lake.

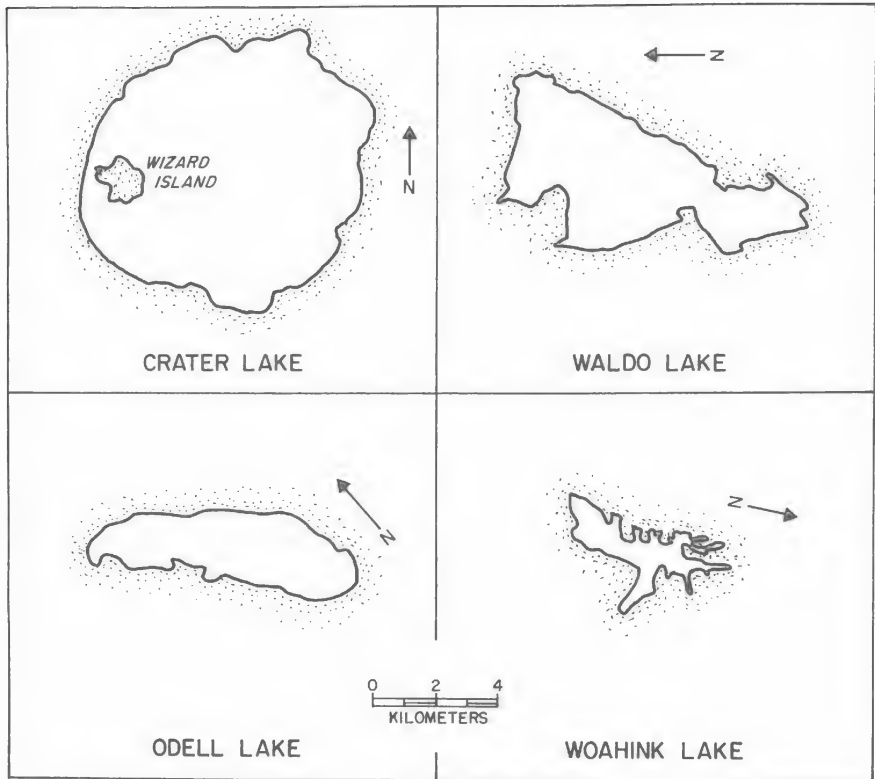


Figure 2. Size and shape relationships among the study lakes, Oregon.

The lake occupies the collapse caldera of volcanic Mt. Mazama. Radiocarbon dating studies by Fryxell (1965) place the approximate age of the lake at 6600 years. Probably, water began to collect in the basin soon after the collapse. But the major accumulation of water has occurred within the last 700 to 1000 years (Nelson, 1967). The re-occurrence of volcanic activity produced an emergent secondary cone (Wizard Island) and two submerged domes on the floor of the basin.

Crater Lake is a closed basin, having no known outlets (Nelson, 1967). Water is lost through seepage (perhaps 20-30 percent of the total loss) and evaporation (Phillips and Van Denburgh, 1968). Of the total amount of water the lake receives, about 78 percent is precipitation falling directly on the lake surface (Phillips and Van Denburgh, 1968). The remaining water input comes from surface runoff (snowslides, sheetwash, meltwater tributaries) and groundwater inflows. No permanent streams enter the lake.

Crater Lake is enclosed by steep caldera walls that ascend from 150 to 610 m above the surface of the lake. In places, the walls rise vertically to the crater rim.

The regolith of the basin is, for the most part, very coarse and permeable. The major constituents include andesite, dacite and dacitic pumiceous ash, and lapilli. Rock debris is generated by the processes of weathering and mass-wasting along the caldera wall. The soils are immature and lack a distinctive horizonation. Only the

upper few inches of the soil profile are darkened by organic matter. Large sections of topsoil are removed periodically by landslides and avalanches (Phillips and Van Denburgh, 1968). Generally, the rates of rock weathering, soil formation, and organic accumulation are impeded considerably by low annual mean temperature (Table 2) and the immaturity of the basin regolith.

Crater Lake, by virtue of its being preserved in a national park, receives extremely limited use. Its primitive condition is maintained by regulations that forbid most recreational activities. Access to Crater Lake is along a precipitous trail that zig-zags for nearly 2 km down the caldera wall. Because of these restrictions, the lake is kept free of most cultural pollutants which fact is exceptional in the United States.

Odell Lake

Odell Lake, situated at the summit of the Cascade Range in the Deschutes National Forest, is 65 km directly north of Crater Lake (Fig. 1). The basin is thought to be a glacial trough closed at the eastern end by a terminal moraine (Russell, 1905). The age of the basin is estimated at 10,000 to 12,000 years.

During the eruptions of Mt. Mazama, volcanic ash was carried northward where it showered onto the loamy soils and andesitic lava in the Odell Lake basin. In time, a mantle of pumiceous ash and lapilli covered the basin to a thickness ranging from 35 to 150 cm. The mantle is coarsely textured and, therefore, is extremely permeable. Of the total volume of pumiceous material, 20 percent to more than 50 percent is comprised of pebbles or "granules" (Wentworth, 1922) larger than 2 mm in diameter. The upper few inches are darkened by organic accumulation. In places, particularly on high angle slopes, the mantle has been removed by weathering and mass-wasting to expose predepositional soils and rock. Because of the texture of the surface layer, sheet-wash runoff is very slow or nonexistent. Subsurface percolation of water through pumiceous and loamy materials is very rapid, thereby facilitating the passage of dissolved minerals into the lake.

Odell Lake is fed by two large, permanent tributaries (*i.e.*, Trapper and Crystal creeks) (Averett and Espinosa, 1968). Both supply the lake with meltwater drained from higher elevations. On a map of Odell Lake, Newcomb (1941) indicated an additional 30 to 35 smaller tributaries. Most of these are shown to enter the lake from the north. The major outlet tributary is Odell Creek which flows eastward for 21 km until it discharges into Davis Lake (Averett and Espinosa, 1968). Groundwater springs are known to exist along the south shoreline (Averett and Espinosa, 1968).

The use of Odell Lake for recreation has grown rapidly, especially since 1960. The lake is easily accessible, and subsequently, numerous homes, campgrounds, and other facilities have developed along the shoreline. Lake users have brought a substantial load of nutrients into the basin that otherwise would not have been available.

Waldo Lake

Waldo Lake is located in the Willamette National Forest, approximately 193 km north of the California-Oregon border, and 175 km inland from the Pacific Ocean (Fig. 1). The lake basin, estimated to be 10,000 to 12,000 years old, is a glaciated depression enclosed by end and lateral moraines.

The regolith of the basin consists mostly of light colored pumice and rounded rock boulders up to 1.5 m in diameter. The materials are well drained and are rapidly permeable. The composition of the bedrock is mainly fractured hard basalts. Depth to bedrock is no greater than 2 m. Bedrock is exposed in many places, especially at the north end of the lake. There, pumice material contains 60 to 70 percent by volume of boulders.

The lake receives no permanent surface drainage. During the spring, however, snowmelt runoff enters the lake through countless temporary streams. Carter *et al.* (1966) suggested that spring seepages may exist on the lake bottom. At the north end, the lake discharges into the North Fork of the Willamette River.

Because of its seclusion and inaccessibility, Waldo Lake received very little use prior to 1969. But during that year, a paved highway was opened leading to several newly constructed campsites situated along the east shore of the lake. Consequently, recreational activities in the Waldo Lake basin were expected to increase considerably.

Woahink Lake

Woahink Lake, a warm monomictic type, is situated on the central coast of Oregon, approximately 165 km west-northwest of Waldo Lake (Fig. 1). The lake basin, typical of many coastal lakes in the state, is a former stream valley obstructed at its mouth by alluviation and sand dune encroachment (Baldwin, 1964). The movement of sand is generally in a northeasterly direction. In places along the west shoreline, the lake is adjoined by dune complexes.

The soil of the Woahink basin consists mostly of sand or sandy loam. The soil west of the lake is described as pure sand (Griffiths and Yeoman, 1938). Further inland, between the east shore of the lake and the Coast Range, the sand grades laterally into a weakly developed sandy loam (Griffiths and Yeoman, 1938). Permeability is extremely rapid; soil fertility is very low.

Woahink Lake is fed by three tributaries that enter from the north and east (McGie and Breuser, 1962). The longest is about 5 km in length. Together, they drain an area of 14.2 km². The lake empties southward into adjacent Siltcoos Lake through the Woahink Creek outlet.

Woahink Lake, like Odell Lake, is very accessible. Recreational use has increased noticeably since 1960. Nearly one-third of the 150 homes along the shoreline were constructed after 1964. Several land development projects have denuded large areas of the watershed.

Methods

Limnological sampling of Crater, Odell, and Woahink lakes was conducted during the summers of 1968 and 1969 (June-September). Waldo Lake was studied during 1969 only. Sampling proceeded from a single index station at each lake, usually under clear skies.

Temperature profiles were determined with an electrical resistance thermistor (Whitney portable model TC-5A, meter scale calibrated in 0.1 units).

Light transmission data were obtained with a submarine photometer (Kahl model 268WA310, selenium barrier-layer type photocell, spectral range in sunlight of 400-640 m μ). Blue, green, and red filters (spectral ranges of 400-550 m μ , 460-660 m μ , and 500-720 m μ , respectively) determined the relative attenuations of these

components of the visible spectrum. Transparency was estimated with a Secchi disk (20 cm diam.). Measurements were taken about 1200 hrs.

Water samples for routine chemical analyses were collected with a 2.5 liter plastic water bottle (Van Dorn) at the surface and from several evenly spaced sampling depths extending to 500 m in Crater Lake, 30 m in Odell Lake, 60 m in Waldo Lake, and 20 m in Woahink Lake. Water analyses, except those for Na, K, Ca and Mg, were handled in a mobile laboratory within 12 hrs after sample collection. pH values were obtained with a model 7 Corning pH meter. Specific conductance was measured with a model RC-16 B2 Beckman conductivity bridge. Total alkalinity was determined colorimetrically using 0.01 N H_2SO_4 as titrant and bromcresol green-methyl red as indicator. Total hardness was determined by EDTA titration. Total dissolved solids (filterable residue) analyses followed *Standard Methods* (APHA, 1965). An atomic absorption spectrophotometer (Perkin-Elmer model 303) was used to analyze samples for Na, K, Ca, and Mg. The Winkler technique (azide modification) measured dissolved oxygen.

Phytoplankton primary productivity was measured *in situ* with ^{14}C . Water samples were collected with Van Dorn bottles at the surface and from several depths extending to 200 m in Crater Lake, 30 m in Odell Lake, 40 m in Waldo Lake, and 18 m in Woahink Lake. A 125 ml portion of water from each sampling depth was inoculated with 1 ml of a stock solution of $\text{Na}_2^{14}\text{CO}_3$ (5.0 $\mu\text{Ci/ml}$) and returned to the depth from which it was drawn. Dark bottles accompanied light bottles at every other depth. Following a four-hour incubation period (1000-1400 hrs), the samples were retrieved and Millipore filtered (AA-type filter, 0.8 μ pore diam.). The filters were stored in a desiccator for one or two days. Each filter was then immersed in 20 mls of a toluene + PPO + POPOP scintillator solution and counted by liquid scintillation (Packard model 2002 Tri-carb Spectrometer). Total available stable inorganic carbon was calculated by multiplying total alkalinity (in mg/1 CaCO_3) by a conversion factor derived from *in situ* temperature and pH data (Saunders *et al.*, 1962). Incident radiation was measured continuously with a Belfort recording pyroheliometer during the incubation periods.

During the summer of 1969, an attempt was made to determine the relative effects of various nutrients on rates of photosynthesis by phytoplankton. Four nutrient stock solutions (KH_2PO_4 , NaNO_3 , NH_4Cl , FeCl_3) were prepared using analytical grade reagents. Every effort was made to avoid contamination and to insure sterile nutrient media. Glassware was rinsed repeatedly with concentrated HCl. Other precautions recommended by Drs. C. R. Goldman (Univ. Calif. at Davis) and J. Shapiro (Univ. Minn., Minneapolis) for the preparation and utilization of nutrient media were followed. Each stock solution was diluted to an initial concentration and dispensed into 20-ml glass ampules. These were sealed by flame, autoclaved, and placed in refrigerated storage. During bioassay experiments, the media were transferred from ampules to 125-ml culture bottles using disposable hypodermic syringes. Three 2½-liter water samples, drawn from a predetermined depth (*i.e.*, 70 m in Crater Lake, 6 m in Odell Lake, 24 m in Waldo Lake, and 4 m in Woahink Lake), were apportioned into 40 125-ml culture bottles. Each subsample was treated with a different concentration of one or more nutrients and 1 ml of the $\text{Na}_2^{14}\text{CO}_3$. For comparative purposes, two additional subsamples (controls) received the $\text{Na}_2^{14}\text{CO}_3$ solution only. The culture bottles (subsamples) were suspended from a rack and

lowered to the depth from which they were drawn. After four hours (usually 1100-1500 hrs), the samples were recovered, Millipore filtered (AA-type), and counted by liquid scintillation.

Water samples were taken at several depths for chlorophyll *a* analyses. Samples were treated immediately with saturated MgCO_3 . Within six-eight hours, a portion of each sample was Millipore filtered (AA-type). Filters were stored in a desiccator and placed in a freezer compartment held at -20°C . Pigment extraction and determination of chlorophyll *a* were conducted in accordance with Strickland and Parsons (1965).

Results

Part of the data gathered during the study suggested that the four lakes fit the broad category of oligotrophy. Secchi depths and other light transmission data (Fig. 3) were indicative of high transparencies due to limited amounts of suspended materials. Low concentrations of dissolved minerals were encountered, particularly in Waldo Lake (Fig. 4, Table 3). The lakes were relatively deep, with steep basin slopes and poorly defined littoral zones. Aquatic vascular plants were not

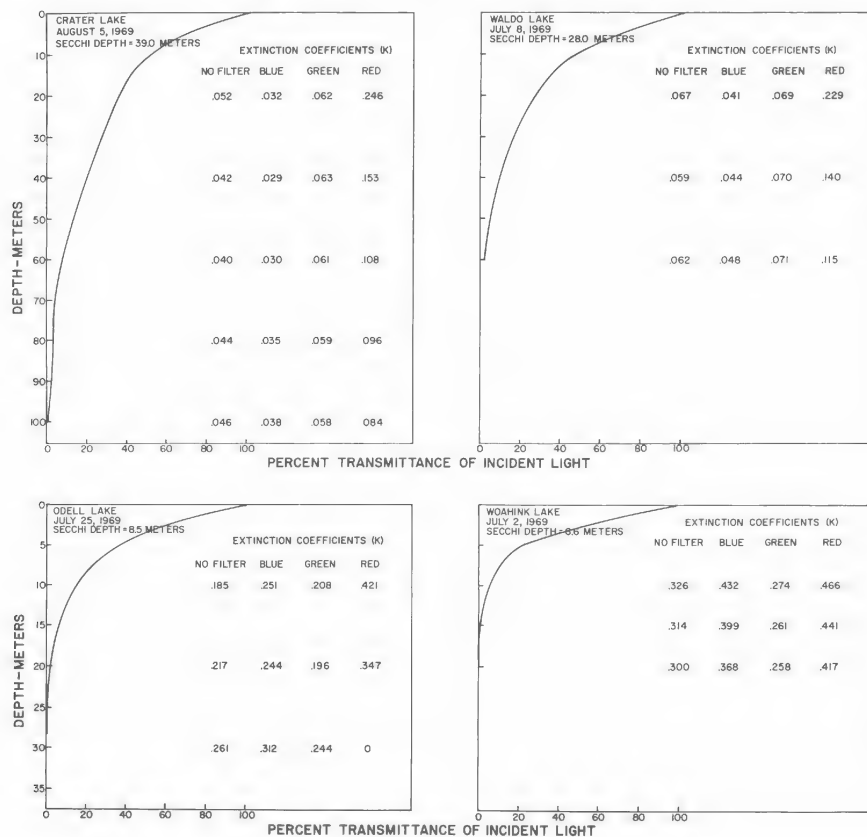


Figure 3. Optical data compared among the study lakes, Oregon.

CHEMICAL FEATURES

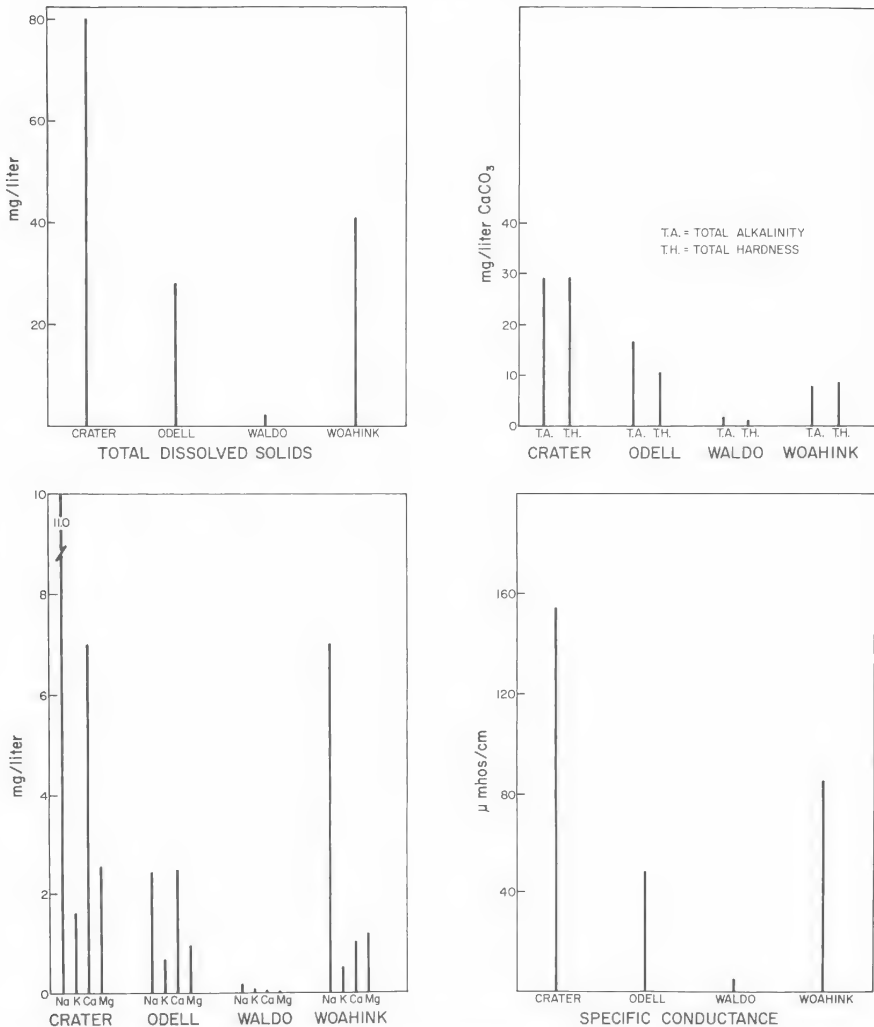


Figure 4. Water chemistry compared among the study lakes, Oregon.

common. The predominant species of fish were rainbow trout, *Salmo gairdneri*, and kokanee salmon, *Oncorhynchus nerka kennerlyi*. Orthograde oxygen curves, low hypolimnetic temperatures, and relatively shallow thermoclines (Fig. 5) were typical of Crater, Odell, and Waldo lakes. The oxygen gradient for Woahink Lake tended to parallel the bottom profile, a feature considered possible in certain small oligotrophic lakes where oxygen is reduced at the mud-water interface (Ruttner, 1953).

The difference in quantities of plankton among the lakes was considerable (Tables 4 and 5). In Waldo Lake, chlorophyll *a* was barely measurable, and vertical tows from

TABLE 3. Concentrations of various nutrient ions reported for Crater and Waldo lakes, Oregon. Values for Odell and Woahink lakes were not available.

	Crater				Waldo	
	1913 ¹	1924 ²	1942 ³	1968 ⁴	1966 ⁵	1969 ⁶
Ammonia-N (mg/l)					< 0.01	
Nitrate-N (mg/l)	0.38	0.47		0.38	0.11	< 0.1
Phosphate-P (mg/l)	0.01	0.10			< 0.01	
Soluble phosphorus (mg/l)			0.014			< 0.002
Silica (mg/l)	18.0	18.0	8.5	18.0		

¹ Van Winkle and Finkbiner (1913). Samples collected at a depth of 2 m.

² Clarke (1924).

³ Uterback *et al.* (1924). Samples collected at several depths to 425 m.

⁴ Phillips and Van Denburgh (1968). Samples collected at a depth of 0.3 m.

⁵ Carter *et al.* (1966). Samples collected at a depth of 3.6 m.

⁶ U.S. Environmental Protection Agency and U.S. Forest Service (1969).

TABLE 4. Concentrations of chlorophyll *a* during August, 1969 compared among the study lakes, Oregon.

Lake	Date	Per Unit Area mg chl. <i>a</i> m ⁻²	Per Unit Volume
			(Averaged for the measured water column) mg chl. <i>a</i> m ⁻³ (average)
Crater	5 Aug 69	35.0	0.175
Odell	7 Aug 69	150.7	5.025
Waldo	6 Aug 69	2.9	0.073
Woahink	2 Aug 69	24.8	1.380

TABLE 5. Numbers of zooplankton collected in vertical tows per cubic meter compared among the study lakes, Oregon, 1969 (Malick, 1971).¹

Lake	Date	Tow depth (m)	Total number of zooplankton per m ³
Crater	17 July 69	100	260
	31 Aug 69	100	575
Odell	10 July 69	30	33,613
	24 July 69	30	19,539
	8 Aug 69	30	27,451
Waldo	8 July 69	60	0.55
	24 July 60	70	0.27
	6 Aug 69	60	1.40
Woahink	1 July 69	16	6,961
	1 Aug 69	16	1,870

¹ Both juveniles and adults are represented. Vertical tows taken with no. 6 mesh net (intake diameter equalled 0.5 m) equipped with a T.S.K. flowmeter.

60-70 m yielded only a few zooplankters per haul. In contrast, Odell Lake supported a much greater biomass of total plankton, including pronounced midsummer algal blooms during 1968 and 1969.

Measurements of phytoplankton net productivity also resulted in comparatively large differences among lakes (Table 6). Productivity estimates for Odell Lake

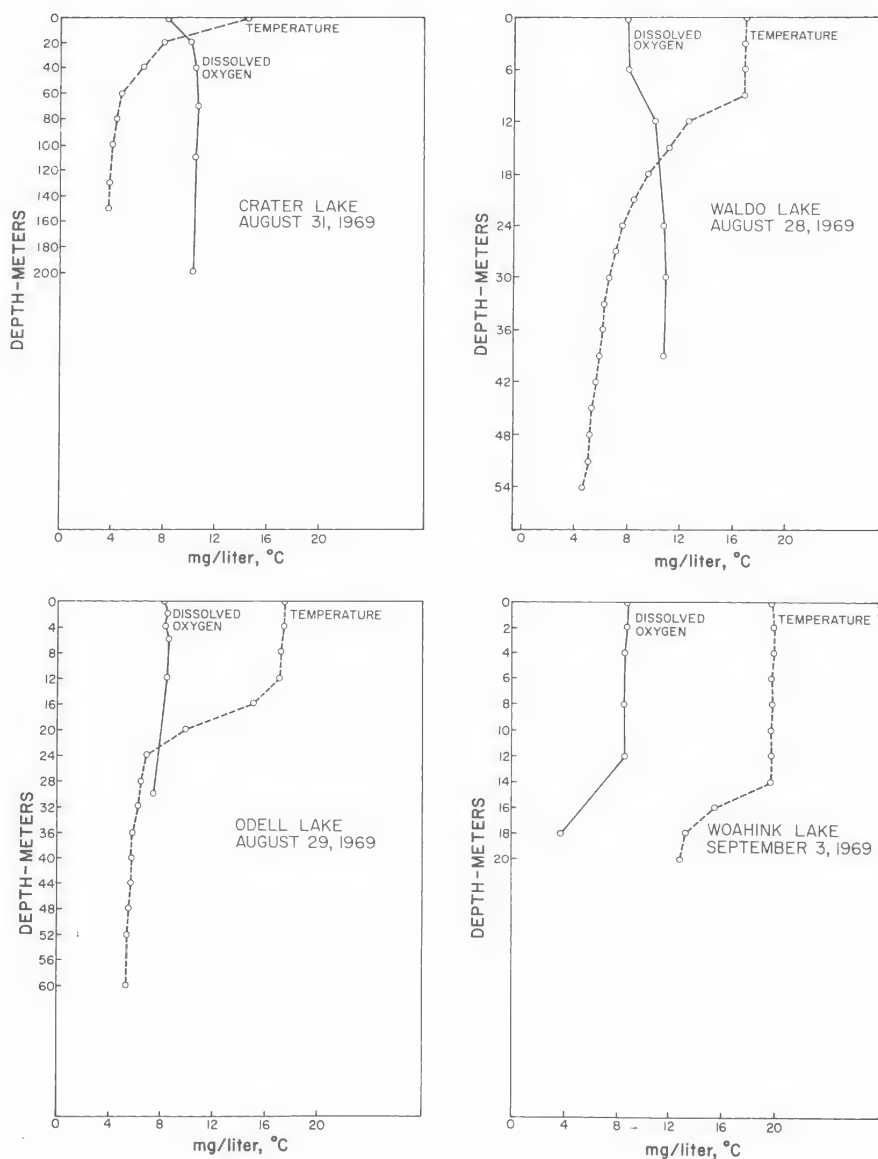


Figure 5. Thermal and dissolved oxygen profiles compared among the study lakes, Oregon.

greatly exceeded those of the other lakes, especially Waldo. Crater and Woahink lakes showed similar productivities per unit area, but were quite different in terms of productivity per unit volume.

The bioassay experiments were not conclusive. Phytoplankton populations in Crater, Odell, and Woahink lakes were virtually unresponsive to nutrient additives. In

TABLE 6. Rates of phytoplankton net production compared among the study lakes, Oregon, 1968-1969.

Lake	Date	Per Unit Area mg C m ⁻² hr ⁻¹	Per Unit Volume (averaged for the measured water column) mg C m ⁻³ hr ⁻¹	Approximate Depth of Maximum Production (P _{max}) (in meters)
Crater	14 Jun 68	27.28	0.19	80
	23 Jul 68	19.66	0.15	60
	27 Aug 68	28.05	0.20	70
	16 Jul 69	21.41	0.11	90
	5 Aug 69	20.68	0.10	115
	31 Aug 69	32.72	0.16	95
Odell	9 Jul 68	170.77	6.10	6
	31 Jul 68	396.79	14.17	1
	13 Aug 68	206.10	7.36	8
	6 Sept 68	196.51	9.83	4
	25 Sept 68	195.16	9.76	2
	10 Jul 69	56.78	1.89	4
	25 Jul 69	149.89	4.99	6
	7 Aug 69	223.03	7.43	3
	29 Aug 69	172.71	5.76	3
	24 Sept 69	112.70	3.75	4
Waldo	21 Jun 69	0.11	<0.01	<1
	8 Jul 69	2.19	0.06	<1
	23 Jul 69	2.26	0.06	<1
	6 Aug 69	4.47	0.11	2
	28 Aug 69	5.05	0.13	8
Woahink	27 Jun 68	37.05	3.09	4
	18 Jul 68	23.14	1.93	6
	7 Aug 68	27.03	1.50	5
	4 Sept 68	22.33	1.86	6
	19 Sept 68	26.43	2.20	2
	2 Jul 69	22.45	1.25	4
	2 Aug 69	36.71	2.04	4
	3 Sept 69	42.55	2.36	4
	28 Sept 69	45.96	2.56	5

Waldo Lake, however, phytoplankton productivity was nearly doubled after adding 0.10 mg/l KH₂PO₄ to the culture bottles during 8 July and 23 July, 1969. This was expected considering the level of phosphorus reported for the lake (Table 3).

Total available stable inorganic carbon (HCO₃⁻ and free CO₂) averaged 8.5 mg/l in Crater Lake, 4.4 mg/l in Odell Lake, 1.3 mg/l in Waldo Lake, and 2.5 mg/l in Woahink Lake. Considering the size of these values, the method used to determine the concentration of inorganic carbon may have been unreliable—particularly with regard to Waldo and Woahink lakes (Johnson and Michalski, 1970). Furthermore, the addition of labelled carrier carbonate (Na₂¹⁴CO₃) to Waldo Lake water samples may have altered photosynthetic rates. If so—and if the additional carbon enhanced photosynthesis during incubation—then the rates of phytoplankton production for Waldo Lake (Table 6) may have been overestimated. Further studies are needed to examine this possibility.

Discussion

Although Rodhe (1969) established rather precise boundaries in graphically depicting the process of lake eutrophication (Fig. 6), he indicated that the transition from oligotrophy to eutrophy is continuous and is not easily broken into finite categories for the purpose of lake typology. On the Rodhe scale (Fig. 6)—which may not apply to lakes in North America—only Waldo Lake is unquestionably oligotrophic. Crater and Woahink lakes occupy positions that are presumably mesotrophic, while Odell Lake is eutrophic, and polluted at that. Furthermore, the 1968 intervals for Odell and Woahink lakes overlap—which illustrates the continuity of lake succession discussed earlier.

Many lake environments in Oregon are being exploited for recreational use, and, as a result, are becoming more productive biologically. The problems that are brought on by increased biological production have been well documented in the literature (Edmondson, 1966; Hasler, 1969). The general effect of artificial enrichment is a shift to higher levels of trophic in respondent lakes. Thus, a typology that was once appropriate may no longer apply to certain lakes that are undergoing rapid eutrophica-

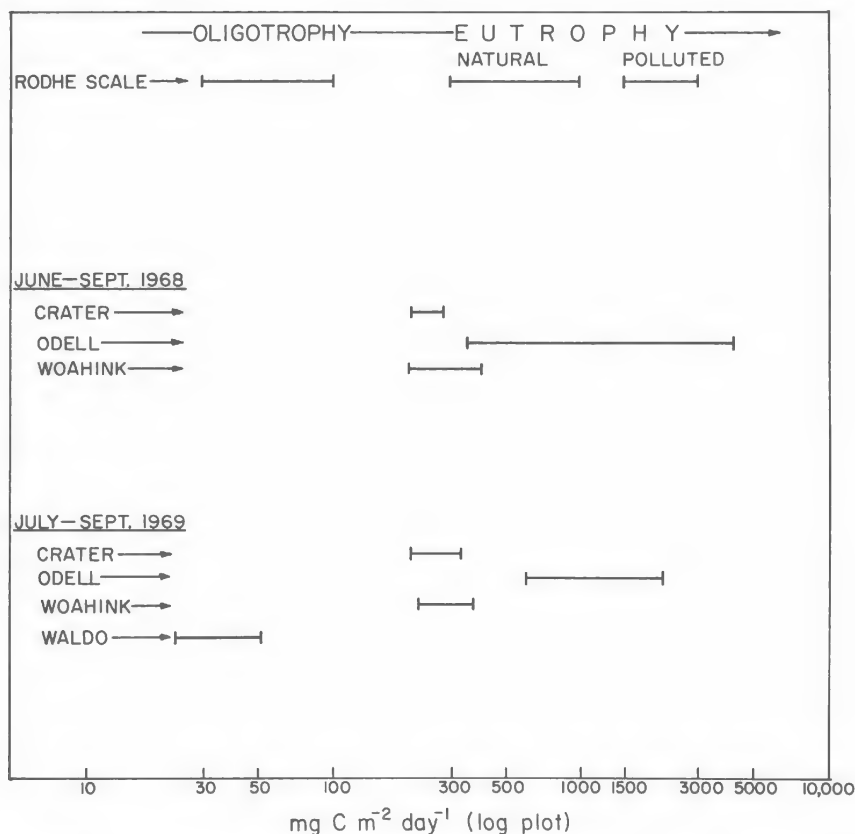


Figure 6. Approximate ranges of phytoplankton primary productivities for the study lakes compared with Rodhe's (1969) scale for oligotrophic and eutrophic lakes.

tion in response to natural and, especially, cultural impositions. In 1940, for example, a limnological survey was conducted on 40 lakes, including Odell Lake, in the then-remote Deschutes River Watershed of central Oregon (Newcomb, 1941). Part of the task was to quantify the benthic and planktonic communities and to classify the lakes accordingly. Each lake was assigned a numerical grade (or index value) that ranged between 1.0 and 2.5. The magnitude of the number depended upon the degree of eutrophy (*i.e.*, the larger the number, the more eutrophic the lake). The number itself was based on a set of limnological conditions that were common to each lake. If a lake received a number between 1.0 and 1.5, for example, it was classified as "oligotrophic"—implying that the value 1.0 represented ultra-oligotrophy. The ensuing ranges of values from 1.6 to 2.0, and 2.1 to 2.5, designated lakes that were "eutrophic" and "advanced eutrophic," respectively. Odell Lake was graded 1.4 (Newcomb, 1941) which placed it slightly within the boundary of oligotrophy. Now, however, the lake would likely fall into one of the higher ranges despite its recent classification (Averett, 1966). The average volume of plankton collected in Odell Lake during September, 1940, was 1.8 mg/m³ of water (Newcomb, 1941). Thereafter the production of plankton increased considerably. In 1968 and 1969, the September hauls yielded, on the average, 20 mg of plankton/m³ (Larson, 1970a).

The relative positions of Waldo, Crater, and Woahink lakes in Figure 6 are of interest, considering how each is being used. Waldo Lake is one of the most oligotrophic freshwater temperate lakes ever encountered. The unusual features of the lake establish a "eutrophication baseline" for predicting the effects of expanded use and subsequent enrichment on other high-quality lakes in North America (USEPA and USFS, 1969).

Crater Lake is relatively free of culturally introduced nutrients, although the supply of nutrients from natural sources may be considerable. Phillips and Van Denburgh (1968) listed three possible means whereby dissolved nutritive material is introduced into Crater Lake: (1) subaerially, from springs and surface runoff, (2) underwater, from the dissolution of soluble materials along the caldera walls, and (3) underwater, from fumaroles and thermal springs. Moreover, precipitation falling directly on the lake may provide significant amounts of nitrogen, phosphorus, and other essential nutritive ions. Since most of the water loss in Crater Lake is through evaporation, it stands to reason that these ions would become more concentrated than in lakes where a sizeable water loss could occur through outflowing tributaries. Together, these sources are responsible for the comparatively high chemical values reported in Figure 4 and in Table 3. Thus, the position of Crater Lake in Figure 6 is perhaps not surprising after all.

A concurrent study of Woahink Lake (Larson, 1970b) indicated a rather low annual rate of phytoplankton production (*i.e.*, 37.2 g C/m²/yr), despite extensive cultural activities in the basin. This is due, possibly, to the interaction of certain climatic and morphometric features that cause the lake to undergo a high rate of flushing and water renewal. Often during the year, portions of the phytoplankton standing crop and nutritive material are removed from the lake. Furthermore, the "new" water that replenishes part of the lake volume may diminish productivity for some time (Findenegg, 1965). Periodic flushing of Woahink Lake is brought about by (1) the small storage capacity of the lake basin as indicated by low seasonal fluctuations in the level of the lake (*e.g.*, variations were less than 0.5 m), (2) moderately heavy

precipitation during the period October through April (approximately 87 percent of the total annual precipitation occurs then), (3) heavy runoff from the high-angle slopes of the surrounding terrain, and (4) a high-volume development (*i.e.*, 1.50) of the basin. Robertson (1954) similarly attributed high rates of flushing in a lake in British Columbia, Canada, to (1) small storage capacity, (2) heavy precipitation (*i.e.*, about 300 cm per year, 60-70 percent occurring during September through March), (3) heavy runoff from a small drainage area (*i.e.*, 9.3 km²), and (4) a high-volume development (*i.e.*, 1.53).

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Heavy Minerals, Pyroclastic Layers, and Alluvial Chronology: An Example

Introduction

Petrographic studies of alluvial sediments penetrated during excavation of an archaeological site on the lower Columbia River, Oregon, show that heavy-mineral suites from the sediments vary systematically within the stratigraphic section. Variation in abundances of some minerals clearly is caused by contribution of minerals from a pyroclastic layer included in the alluvium. Abundances of other minerals not contributed by the pyroclastic layer also vary stratigraphically, but the cause is not clear.

Strata in archaeological sites commonly are dated through artifacts or radiocarbon; pyroclastic layers can be dated and correlated over long distances (Wilcox, 1965; Nowak, 1968; Kittleman, in preparation); and alluvial strata in general can be dated in various ways (Haynes, 1968). Conjunction of such chronometry with stratigraphic variations in heavy-mineral suites offers information useful in studies of the evolution of drainage basins, alluvial chronology, stream terraces, and marine dispersal of fluvial sediment.

This paper reports a study of just one site in a complex drainage basin, so the conclusions that may be drawn are limited. The results are presented in the belief that they may have some general importance.

The alluvial stratigraphic section examined was exposed during excavation of the Wildcat Canyon archaeological site [35 GM 9¹] (Cole, 1968, and references cited therein). The site is on the south bank of the Columbia River about 20 km (13 mi) downstream from Arlington, Oregon, within the area now flooded by John Day Reservoir (Fig. 1). Excavation there exposed a section about 4 m thick between bedrock of Yakima Basalt (Columbia River Group) and the modern surface. In general the sediments are unconsolidated, yellowish-brown² to yellowish-gray, fine- to very fine-grained sands, silts, and sandy silts. Median grain size ranges from about 30 to 160 μm ; it is greatest near the bottom of the section and becomes gradationally less toward the top. Stratification is gradational and relatively inconspicuous, and neither laminations nor cross-strata are apparent. Sediment in the lower part of the section probably was derived from channel deposits of the Columbia River, but may have been deposited at the site by subsequent incorporation into riverine dunes. Sediment in the upper part probably is mainly silty overbank deposits that have been reworked and redeposited by wind. Sediment may have been contributed by colluvial deposition or by Wildcat Creek, an ephemeral tributary now 50 m east of the site, but there are no strata which

¹ Site-numbering system of the Museum of Natural History, University of Oregon.

² Rock-Color Chart (Goddard and others, 1951).

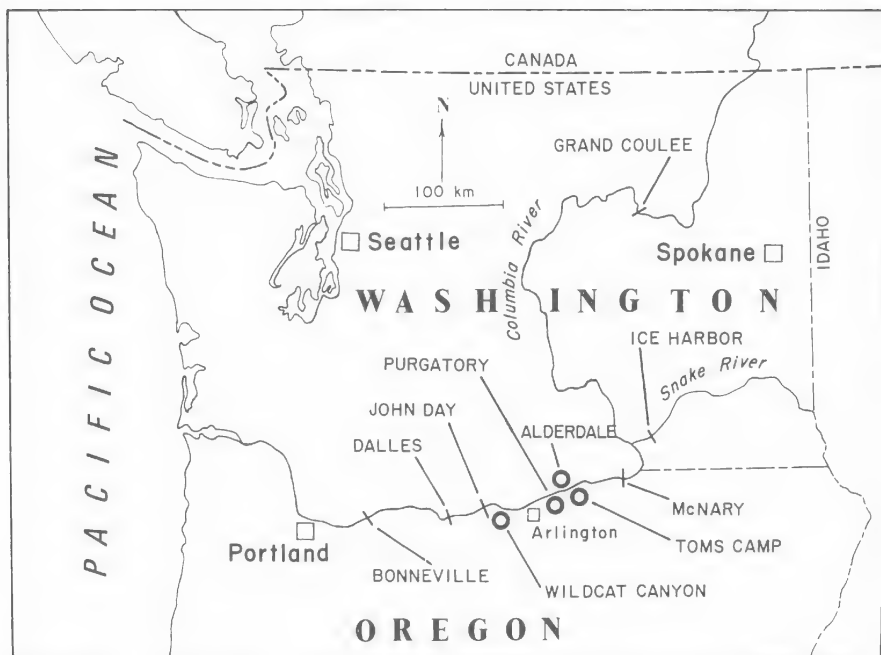


Figure 1. Regional index map. Archaeologic sites are indicated by bold circles; dams for reservoirs mentioned in the text are shown by short bars struck across stream.

seem to indicate discrete depositional events from these sources (Kittleman, ms.). The stratigraphic section is shown graphically on Figure 2, where strata are designated with Roman numerals. The stratigraphy shown was determined prior to the heavy-mineral study. Included are two buried soils, one of which is represented by a horizon of soil-carbonate (Kittleman, ms.), and there is a layer of volcanic ash (stratum IV) from the climactic eruption of Mount Mazama, 350 km to the southwest in the Cascade Range of Oregon (Randle, Goles, and Kittleman, 1971).

Radiocarbon and archaeologic methods indicate that the oldest sediments in the section were deposited more than 10,000 years ago (Cole, 1967), and strata at the top of the section contain artifacts characteristic of a period about 1750 A.D. (Cole, personal communication, 1971). The eruption that produced the pyroclastic layer (stratum IV) happened about 6600 (Fryxell, 1965) to 7000 years ago (Randle, Goles, and Kittleman, 1971; Kittleman, in preparation). Chronometric data from the site are still being studied by archaeologists, and it would be premature for me to attempt to assign ages to other individual strata.

Procedure

Samples were collected at the archaeologic site by taking sediment from the walls or floors of excavations. The stratigraphic positions of samples used for this study are indicated by black triangles near the left edge of Figure 2. Samples generally weighed 50 to 100 g and represent a stratigraphic interval of about 5 cm, but samples 5,

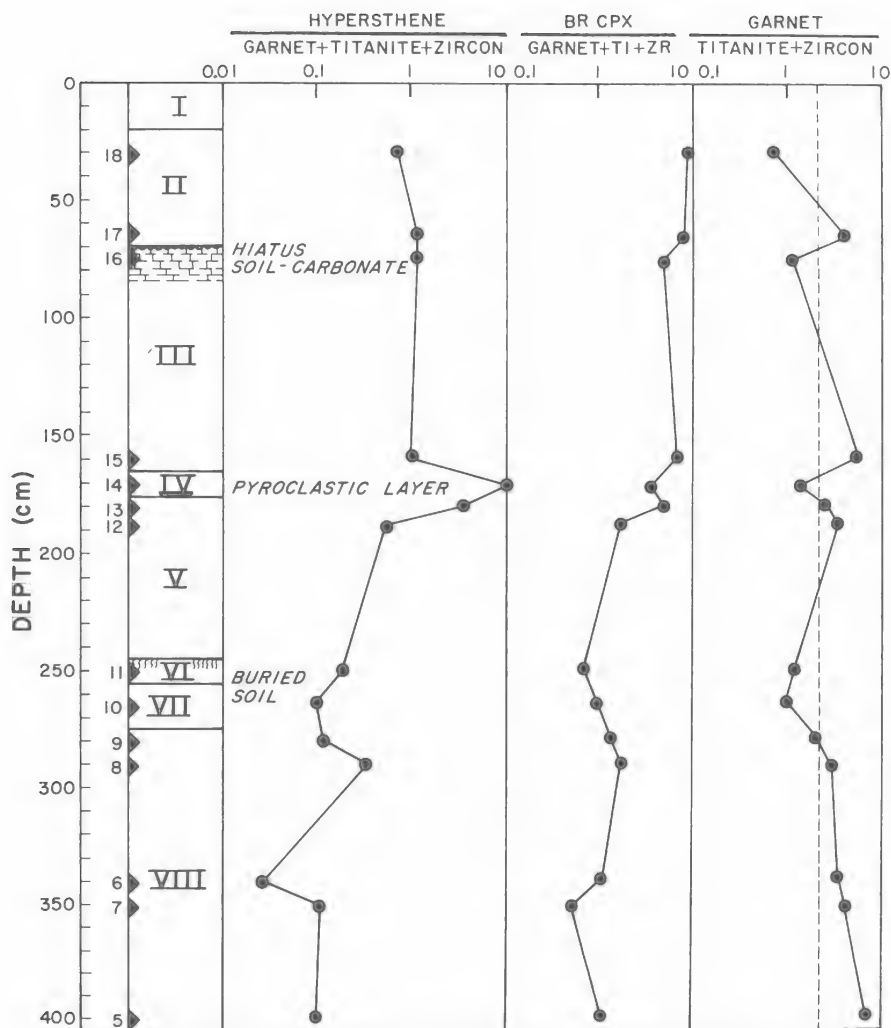


Figure 2. Stratigraphic diagram for Wildcat Canyon archaeological site. A generalized stratigraphic section is shown on the left, where individual strata are denoted by Roman numerals. Stratigraphic variation of three abundance-ratios of heavy minerals is shown. The black triangles indicate the stratigraphic positions and numbers (Table 1) of samples. BR CPX means brown clinopyroxene; TI, titanite; and ZR, zircon.

10, and 11 were collected under less well-controlled conditions from the floor of the excavation below the seasonal water table. Figure 2 is a generalized composite of sections from three locations within the site, because a complete section was never exposed at a single location.³ Distances between the individual sections range from 15 to 50 m.

³ The sampled sections are at locations 32x/22y, 34x/8y, and 78x/3y in the system of coordinates used during excavation.

Sediment between 60 and 500 μm in size, obtained by sieving and settling, was used for heavy-mineral analysis. Heavy minerals were extracted by a method modified from that of Fessenden (1959). A sample is put in a 50-ml polyethylene centrifuge tube with bromoform of specific gravity of 2.90. After centrifugation, bromoform at the bottom of the tube is frozen by partially immersing the tube in a mixture of ethanol and dry ice. Light minerals are poured from the top of the tube, then the remaining bromoform is thawed and the heavy minerals are recovered by filtration. No formal test of the efficiency of recovery was made, but I concluded from my experience with these and similar samples that centrifugation produces superior separation, because the heavy minerals in these fine-grained sediments settle slowly in the conventional open funnel and are disturbed by convection currents in the bromoform.

Portions of heavy-mineral separates were prepared with a microsplitter and mounted in Canada balsam. Grains in the range of sizes from 60 to 500 μm were mounted together, following van Andel (1950). Abundances of heavy minerals were obtained in terms of number-percent through ribbon-counting (Galehouse, 1969). Mica was not counted. Counting was continued until 500 grains other than opaque minerals, altered grains, and unidentified grains had been tabulated. The total count thus usually is about 1000.

Results

Heavy-mineral suites of the Columbia River sediments that were examined are dominated by opaque iron-titanium oxides (here called magnetite), hornblende, clinopyroxene, hypersthene, and garnet. There are small amounts of titanite, zircon, epidote, apatite, kyanite, and other minerals (Table 1). With minor exceptions, essentially the same inventory is reported by Kulm and others (1968) and by Whetten, Kelley, and Hanson (1969). There are several varieties of hornblende and of clinopyroxene, which are distinguished as indicated in Table 1, and there are several varieties of garnet, principally pink and colorless, which are not distinguished. The terms green hornblende and brown hornblende both include minerals of various pleochroic schemes, but it was not feasible to distinguish them during counting because of intergradation. The samples contained 2 to 13 percent heavy minerals.

In assessing abundances of heavy minerals in sequences where there may be variations from weathering and inconsistent source, it is convenient to compare the abundances of minerals that are expected to be variable with the abundances of minerals, called *index minerals*, that are expected to be relatively invariant and resistant to weathering (Brewer, 1964). No ideal index minerals are present in the suites from Wildcat Canyon. Zircon, titanite, kyanite, rutile, and tourmaline are resistant (Brewer, 1964), but they are individually so rare that estimates of their abundance are attended by unacceptably large sampling errors. Garnet, however, is consistently present in reasonable amounts, and I have included it as an index mineral from necessity, even though its stability is equivocal (Raeside, 1959; Brewer, 1964). I use summed abundances of GARNET + TITANITE + ZIRCON as an index to measure variation in abundances of other minerals. The constancy of the index itself is assessed by the

garnet ratio $\left(\frac{\text{GARNET}}{\text{TITANITE} + \text{ZIRCON}} \right)$. One must recognize, however, that the abundances of these minerals are low, and sampling errors correspondingly large, for

TABLE 1. Abundances of heavy minerals (percent).

		Green Hornblende	Brown Hornblende	Magnetite*	Green Clinopyroxene	Brown Clinopyroxene	Garnet	Hyperssthene	Altered Grains	Rock Fragments	Titanite	Zircon	Epidote	Kyanite	Olivine	Apatite	Rutile	Tourmaline	? Diopside	Zoisite Group	? Enstatite	Limonite	Other Minerals ⁺ and Unknowns
1	modern	4.9	11.2	25.8	8.0	15.1	0.7	9.8	10.4	9.8	0.2*	0.1	0.8	0.2	0.1	0.6	nil	nil	nil	0.1	nil	nil	2.3
2	modern	7.5	7.4	22.3	4.4	21.3	2.0	3.6	10.5	15.0	0.6	nil	0.7	nil	nil	0.2	0.1	nil	nil	nil	nil	nil	4.3
3	modern	11.8	5.6	26.8	4.9	17.2	0.7	1.0	14.0	8.8	1.3	0.7	0.2	0.4	nil	1.2	nil	nil	nil	nil	nil	nil	5.4
4	test-pit	12.2	6.3	24.1	2.1	14.9	2.3	0.7	15.2	12.7	1.4	0.3	1.0	0.2	0.3	1.0	nil	0.1	nil	nil	nil	nil	3.7
5	Wildcat Canyon	22.4	7.8	11.8	3.5	9.8	7.9	0.9	20.2	5.5	0.8	0.3	0.5	1.1	nil	1.0	nil	nil	0.4	0.2	nil	nil	6.1
6	Wildcat Canyon	19.1	6.5	12.1	5.6	10.8	7.3	0.3	17.3	8.1	2.0	0.1	0.1	0.9	nil	2.0	nil	nil	1.3	nil	nil	nil	6.4
7	Wildcat Canyon	20.9	5.6	17.0	5.2	6.3	9.9	1.4	16.8	2.4	2.2	0.2	2.0	0.2	nil	0.8	nil	nil	0.8	nil	0.8	nil	7.0
8	Wildcat Canyon	19.5	3.7	12.6	4.1	9.4	4.0	1.8	25.9	9.7	1.1	0.2	0.5	0.6	nil	0.9	nil	0.1	0.5	nil	0.1	nil	5.2
9	Wildcat Canyon	24.0	5.7	20.4	3.8	6.3	3.2	0.6	18.6	3.4	1.5	0.1	1.3	0.2	nil	1.8	nil	0.1	0.9	0.1	nil	nil	7.8
10	Wildcat Canyon	13.4	1.7	23.9	2.2	2.0	1.0	0.2	10.8	5.3	0.9	0.1	0.3	nil	nil	0.5	0.1	0.1	nil	0.1	nil	34.4	2.8
11	Wildcat Canyon	34.0	5.2	22.2	3.8	2.4	1.7	0.6	13.4	4.8	1.2	0.2	nil	0.2	nil	1.2	0.1	nil	0.3	nil	nil	2.4	6.2
12	Wildcat Canyon	12.4	4.2	27.1	4.9	12.7	5.6	4.0	13.7	9.3	1.0	0.5	nil	nil	0.1	nil	0.1	nil	0.8	nil	0.2	nil	3.3
13	Wildcat Canyon	7.2	5.2	40.3	5.9	9.0	1.3	6.7	15.2	5.2	0.3	0.2	0.2	nil	0.3	0.2	0.1	nil	0.3	0.1	nil	0.4	2.0
14	Wildcat Canyon	11.6	3.6	31.0	6.6	5.2	0.8	14.4	4.4	20.2	0.6	nil	nil	nil	nil	0.4	nil	nil	nil	nil	nil	nil	1.2
15	Wildcat Canyon	13.1	4.4	27.1	6.0	18.0	2.3	2.8	14.6	7.9	0.4	nil	nil	nil	0.1	nil	0.1	nil	nil	0.1	nil	0.3	2.7
16	Wildcat Canyon	11.4	2.8	40.1	4.9	12.6	1.3	3.0	15.7	2.5	0.5	0.7	nil	0.1	0.1	nil	0.1	nil	0.1	nil	0.1	nil	4.0
17	Wildcat Canyon	14.8	2.8	24.6	5.4	16.7	1.6	2.4	20.1	5.2	0.4	nil	0.4	nil	0.1	nil	nil	nil	nil	nil	nil	nil	5.0
18	Wildcat Canyon	15.7	2.5	28.0	6.3	21.1	1.0	1.8	13.6	4.1	0.7	0.7	0.1	0.1	nil	0.1	0.1	nil	nil	nil	nil	nil	4.1
19	Alderdale	17.6	2.6	20.2	5.0	11.7	0.8	0.6	23.4	12.0	0.4	0.1	0.3	nil	0.1	0.2	nil	nil	0.1	nil	nil	nil	5.0
20	Alderdale	22.1	2.8	20.9	3.7	10.8	1.0	1.8	21.0	8.2	0.4	0.1	0.4	0.1	0.4	0.5	0.1	0.1	0.3	nil	nil	nil	5.4
21	Alderdale	21.8	2.3	18.8	2.9	14.0	1.4	1.7	21.8	5.9	1.4	0.1	nil	0.4	nil	0.6	nil	nil	0.2	nil	nil	nil	6.6

* Opaque iron-titanium oxides.

^x Abundances given as tenths of a percent of course are very imprecise; they are presented only to indicate the number of grains actually counted (0.1 percent signifies that one grain was seen in a count of 1000).⁺ Staurolite, piedmontite, topaz, monazite, and sideromelane.

example, roughly 30 percent (two standard deviations) of the amount reported for garnet. Ratios are intractable for parametric statistics (Griffiths, 1967; Curtis, 1941), and it is difficult to test the significance of their variations rigorously. In this study I rely on inspection of the data supplemented by a nonparametric test. Bearing these limitations in mind, three ratios are plotted with respect to stratigraphic position in

Figure 2: the *garnet ratio*, the *hypersthene ratio* $\left(\frac{\text{HYPERSTHENE}}{\text{GARNET} + \text{TITANITE} + \text{ZIRCON}}\right)$ and the *clinopyroxene ratio* $\left(\frac{\text{BROWN CLINOPYROXENE}}{\text{GARNET} + \text{TITANITE} + \text{ZIRCON}}\right)$.

In Figure 2, the hypersthene ratio ranges from 0.1 to 0.3 in stratum VIII, increases to 10 in the pyroclastic layer (stratum IV), and remains about 1.0 in the overlying strata. With respect to stratum VIII, the hypersthene ratio is one hundred-fold greater in the pyroclastic layer and ten-fold greater in strata II and III. Likewise, the clinopyroxene ratio increases ten-fold between the bottom and top of the section. For purposes of comparison, the stratigraphic section is divided into *older alluvium* (layers below stratum V) and *younger alluvium* (stratum V and above). Nonparametric statistical tests indicate that both the hypersthene ratio and the clinopyroxene ratio are significantly different in the younger alluvium than in the older alluvium, but that there is no such difference in the garnet ratio.⁴ The ranges of variation are, respectively, about 58 percent and 28 percent greater than the range of the garnet ratio. That is, the garnet ratio is the most conservative. More importantly, the garnet ratio does not change progressively with respect to stratigraphic position, but varies about its geometric mean, which is indicated on Figure 2 by the dashed line. Garnet, titanite, and zircon thus seem to be reasonable index minerals, at least with respect to progressive stratigraphic changes; however, my data are insufficient to determine what proportion of the variation of the garnet ratio may be caused by inhomogeneities in the sediment and what proportion by sampling error.

The pyroclastic layer (Fig. 2) is rich in hypersthene and contributes grains of that mineral to strata just below and a considerable distance above it. The heavy-mineral suite of the Mazama ash, with which this pyroclastic layer is correlated, is 41 percent magnetite, 35 percent hypersthene, 13 percent green and brown hornblende, and 10 percent green clinopyroxene (Randle, Goles, and Kittleman, 1971). At Wildcat Canyon, the Mazama pyroclastic layer is fine-grained, crystal-poor vitric ash that appears to be pure on visual inspection, but its heavy-mineral suite is adulterated with minerals from adjacent alluvial strata (Table 1, analysis 14). Exchange of mineral grains among strata probably arises from the combined effects of prehistoric human activity, burrowing animals, and aeolian reworking. Hypersthene in the ash characteristically has bubble-wall texture (Fisher, 1963) or has jackets of adherent glass, and it is recognizable as pyroclastic in strata above and below the pyroclastic layer.

The clinopyroxene ratio also increases ten-fold between the bottom and top of the section (Fig. 2), but there is no brown clinopyroxene in Mazama ash, and it is not clear why the abundance of brown clinopyroxene should vary as it does. The clinopyroxene probably is derived from basalt, for it resembles that seen in thin sections

⁴One-tailed Kolmogorov-Smirnov test at the 95 percent level of confidence, using common logarithms of ratios. (Siegel, 1956, pp. 127-136.)

of Yakima Basalt, in which the Columbia River Gorge is cut, and, in the sediments, it commonly occurs in rock fragments together with plagioclase, magnetite, or dark glass.

The curve for each ratio (Fig. 2) has an inflection indicative of diminished abundance of hypersthene, brown clinopyroxene, or garnet, respectively, at the level of the buried soil at about 250 cm depth. Both hypersthene and clinopyroxene weather readily (Brewer, 1964) and garnet may do so (Raeside, 1959), so the inflections perhaps indicate diminution in the abundances of these minerals by weathering. The length of time available for such weathering cannot be determined, because we know only that stratum VIII and, by inference, strata VII and VI were deposited more than 10,000 years ago (Cole, 1967; and personal communication, 1971).

Heavy-mineral suites from the section at Wildcat Canyon are compared to suites from nearby localities in terms of major constituents on Figure 3. The components of

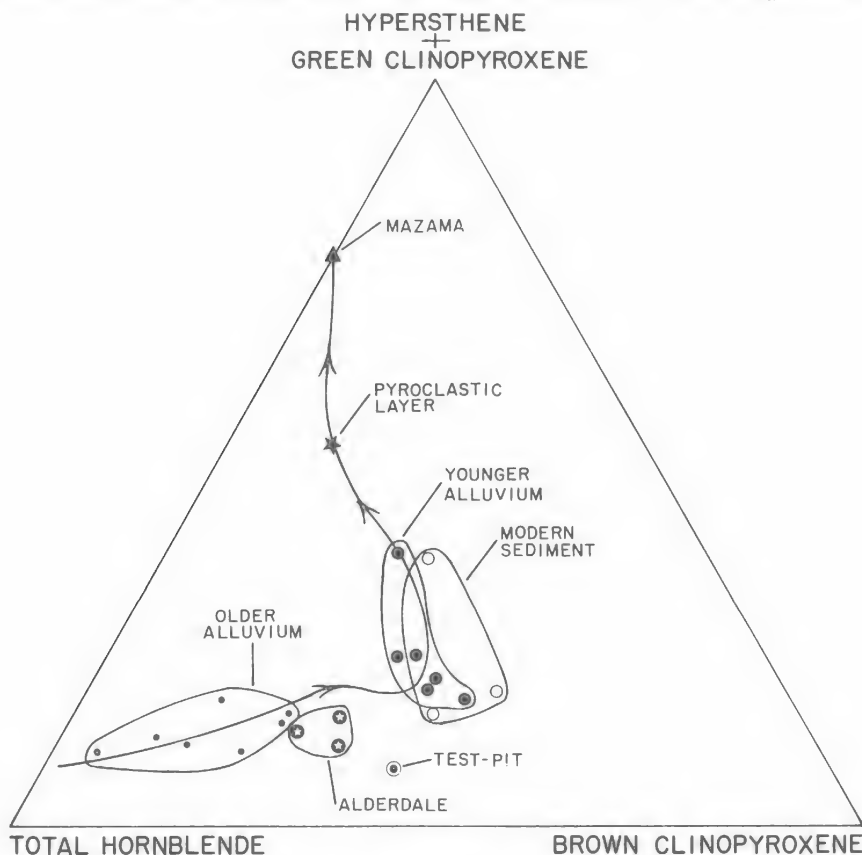


Figure 3. Ternary diagram of principal pyroclastic and detrital minerals. Small dots represent analyses of older alluvium at Wildcat Canyon (stratum VI and older); large dots, younger alluvium (stratum V and younger); circles, modern sediment of Columbia River; white stars, alluvium from Alderdale archaeological site. The encircled dot represents alluvium from the engineering test-pit; the star, the pyroclastic layer at Wildcat Canyon; and the black triangle, unadulterated Mazama ash. The sinuous line suggests the evolution of the composition of heavy-mineral suites with increasing addition of minerals from Mazama ash.

the ternary diagram represent the major constituents of the sediments in general (hornblende and brown clinopyroxene) and the distinctive constituents of Mazama ash (hypersthene plus green clinopyroxene). The heavy line indicates an evolutionary trend of the Wildcat Canyon suites with increasing additions of constituents from Mazama ash. The composition of unadulterated ash is shown also. Suites from the younger alluvium at Wildcat Canyon (above stratum VI) coincide with those from modern sediment of the Columbia River, but suites from the older alluvium are distinct. The assemblage from the engineering test-pit is thought to represent ancient bed material, perhaps left by late glacial scabland flooding (Bretz, Smith, and Neff, 1956). Suites from the Alderdale site appear to resemble those from the older alluvium of the Wildcat Canyon section, yet archaeologic data (D. L. Cole, personal communication, 1970) indicate that all strata excavated at the Alderdale site were deposited after the Mazama eruption, and therefore the mineral suites should resemble those from the younger alluvium at Wildcat Canyon. Failure of this particular diagram to make the predicted distinction may be caused, in part, by the presence of hornblende in both Mazama ash and in pre-Mazama sediments, which makes the ratio of HORNBLENDE to HYPERSTHENE + GREEN CLINOPYROXENE ambiguous.

Comparisons among suites from the several localities are made in what is perhaps a more refined way in Figure 4. Here the suite from the engineering test-pit is

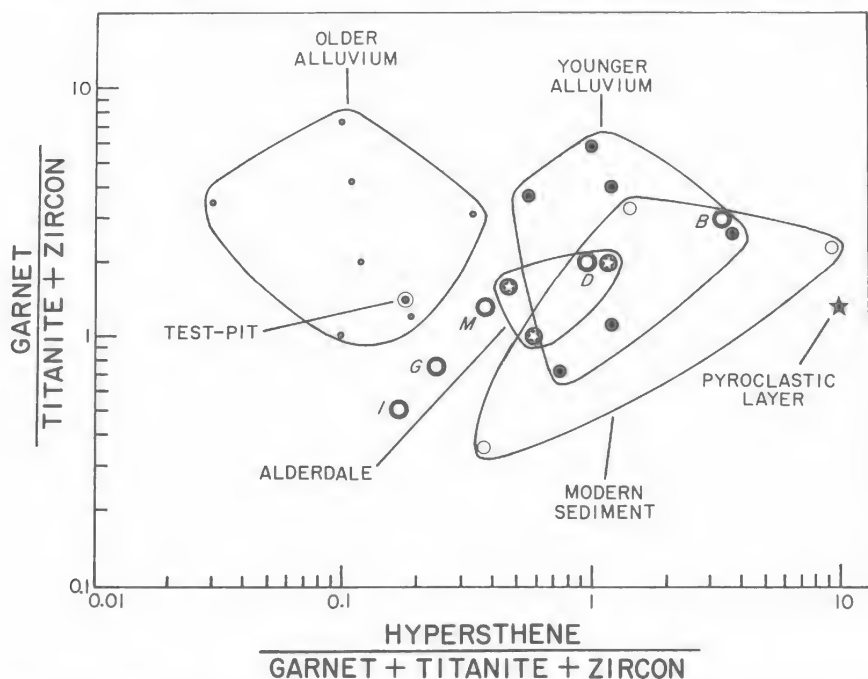


Figure 4. Abundance-ratio diagram for heavy-mineral suites. Variation of the hypersthene ratio is shown. The bold circles represent analyses of heavy minerals in bottom sediments in reservoirs on the Columbia River (Whetten, Kelley, and Hanson, 1969). I stands for Ice Harbor reservoir; G for Grand Coulee; M for McNary; D for Dalles; and B for Bonneville. The other symbols are the same as those on Figure 3.

represented in the older group, and those from Alderdale, in the younger. Some other points that represent heavy-mineral suites of bottom sediments in reservoirs on the Columbia River (Whetten, Kelley, and Hanson, 1969) also are plotted, and it is noteworthy that these suites seem to have progressively more hypersthene in the downstream direction toward the source of Mazama ash; for example, compare the suite from Ice Harbor Reservoir (I) with that from Bonneville Reservoir (B).

Data are plotted in the same way for the clinopyroxene ratio on Figure 5, where older and younger groups again can be distinguished. Here, however, the point that represents the suite from the engineering test-pit falls within the younger group, rather than the older, as on Figure 4, and this ambiguity serves as a reminder that the meaning of the clinopyroxene ratio is yet to be established. It has been determined that, among the heavy-mineral suites from Wildcat Canyon, those from the older alluvium are relatively poorer in brown clinopyroxene than those from the younger alluvium. The objection may be made that brown clinopyroxene could have been diminished in older sediments by intrastratal solution and weathering, but the persistence of hornblende in the older alluvium suggests otherwise. Further objection may be made that the older alluvium is more coarse-grained than the younger, and mineralogical differences might be ascribed to the influence of grain-size alone, but if

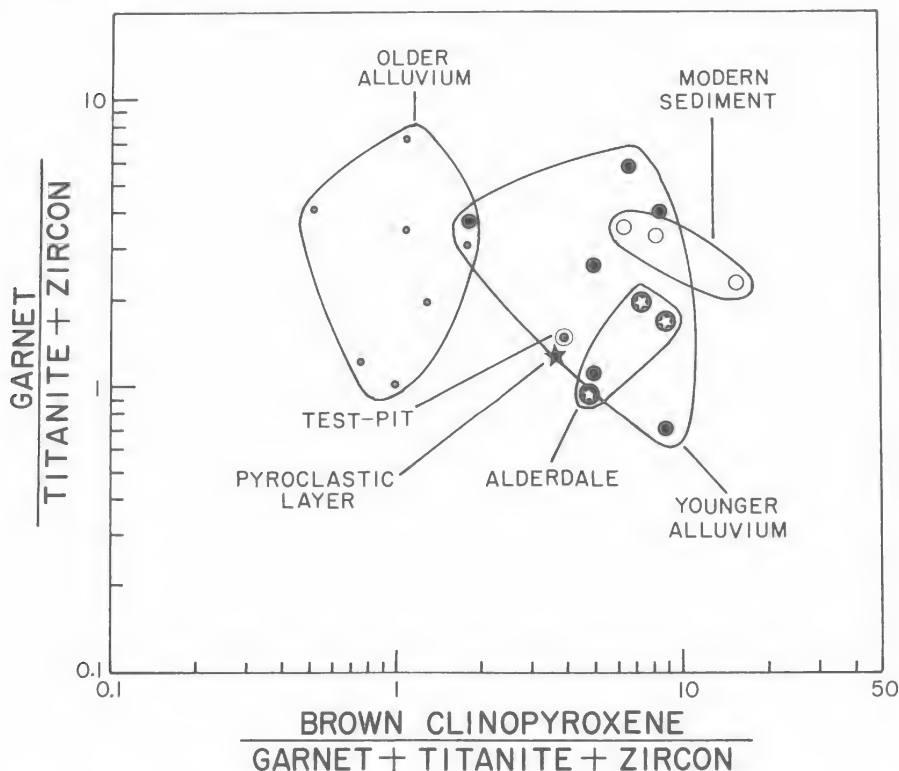


Figure 5. Abundance-ratio diagram for heavy minerals that shows variation of the clinopyroxene ratio. The symbols are the same as those on Figure 3.

modern sediment is also considered, then the median grain-size of the younger alluvium and modern sediment together ranges from about 30 to 150 μm , whereas that of the older alluvium ranges similarly from 90 to 160 μm .

It is reasonable to suppose that much of the brown clinopyroxene in heavy-mineral suites at Wildcat Canyon is derived through weathering of the Yakima Basalt, but; granted that assumption, it is then difficult to understand why the older alluvium at Wildcat Canyon should be deficient in brown clinopyroxene. Possible sources of sediment at Wildcat Canyon are alluvial deposition from the Columbia River or from Wildcat Creek, colluvial deposition, and aeolian deposition of reworked alluvial sediment. Wildcat Creek, which drains from a basaltic escarpment, must supply basaltic detritus, but no discrete strata attributable to that source were recognized at the Wildcat Canyon site. Local influx cannot wholly explain the enhanced abundance of brown clinopyroxene in the younger alluvium, because large clinopyroxene ratios are shared by heavy-mineral suites from Alderdale, as well as those from modern sediment (Fig. 5). Petrographic and grain-size studies at Wildcat Canyon and nearby localities (Kittleman, ms.) indicate that alluvial sediments of the Columbia River are cycled amongst channel, overbank, and aeolian environments; such a process would furnish ample opportunity for thorough intermixing of constituents. A possible interpretation of the alluvial sequence at Wildcat Canyon is that the homogeneous, massive, older alluvium represents only a single event, earlier than the Mazama eruption, which caused influx of sediment poor in basaltic clinopyroxene from the upper course of the Columbia River (Whetten, Kelley, and Hanson, 1969), whereas the silty younger alluvium represents overbank and fine-grained channel deposits variously reworked by wind. The Mazama pyroclastic layer would contribute distinctive mineral grains to younger strata, not only through local mixing, but also through incorporation of constituents from the widespread pyroclastic layer into later alluvium arriving from upstream.

Discussion

The works of Rittenhouse (1943, 1944) and of van Andel (1950) show the great complexity of relations among heavy minerals in individual stream systems, in both along-stream and across-channel directions. Consideration of heavy-mineral assemblages in alluvial sequences adds yet another dimension. The Columbia River basin itself is a complex system that contains large tributaries and several different terranes (Whetten, Kelley, and Hanson, 1969). This study of but a single locality can offer little more than a few tantalizing suggestions.

The data given here show that older alluvium at the Wildcat Canyon site has distinctive heavy-mineral suites which are relatively poor in both hypersthene and brown clinopyroxene, and that suites from the younger alluvium are relatively rich in these constituents and are concordant with suites from bottom sediments of reservoirs of the lower course of the Columbia River, modern channel deposits, and young deposits at the Alderdale archaeologic site. The influence of the Mazama pyroclastic layer with respect to the abundance of hypersthene seems unequivocal. This layer is present throughout a large part of the Columbia River basin (Wilcox, 1965). Upland deposits and layers of it in alluvial banks are reservoirs of characteristic heavy minerals that must contribute to the modern bed-load of the Columbia River. Variation in the abundance of brown clinopyroxene, though conspicuous, is not yet explained. If these contrasts in any significant degree portray temporal variation in

sediments of the Columbia River generally, then, for example, the mineral assemblages in modern sediments of the Columbia River cannot be used as a guide to trace marine dispersal of Columbia River sediments during glacial and early post-glacial times.

More generally, the relationships seen suggest some applications of heavy-mineral analysis on the small temporal scale of the Quaternary, as in alluvial chronology as applied by Haynes (1968), in which particular phases of alluviation may be marked by characteristic pyroclastic debris or by assemblages derived glacially from distant areas. Wolman and Miller (1960) have suggested that most geomorphic work is done by events of moderate magnitude and frequency. Markers such as pyroclastic minerals stored in alluvium will be eroded from banks during events of moderate to large magnitude and deposited farther downstream to form an alluvial and mineralogic record of such events and their frequency.

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Phosphorus and Algal Growth in the Spokane River

In recent years there has been an increasing awareness of the deteriorating quality of our natural water systems. For the most part the occurrence of massive, and often offensive, algal blooms in our rivers and lakes is due to increasing nutrient enrichment. The major sources of these nutrients are urban and rural runoff, precipitation, groundwater, and domestic and industrial wastes. The discharge of wastewater, after various degrees of treatment, into a receiving body of water can trigger algal blooms and accelerate eutrophication. Determination of nutrients which might constitute the limiting factor(s) to algal growth in a particular body of water is essential in order to remove those nutrients from wastewater discharges.

Phosphorus, a key element in aquatic fertilization, is often in high concentrations in wastewater effluents. While it is clear that the growth of algae is made possible by adequate supplies of phosphorus, its relative importance as a controlling factor in biological production is often debated.

The problem under consideration is whether phosphorus is an important regulator of algal growth in the Spokane River in eastern Washington. Since the river can and does support a good algal crop, the question becomes whether ambient phosphorus levels are sufficiently high that additions of wastewater phosphorus would result in no substantial increase in total biomass, or the alteration of the algal compositions toward the more undesirable forms.

Often the extent of aquatic pollution has been measured by chemical and physical parameters only. Chemical analysis of the water, however, does not necessarily indicate potentially limiting nutrients, since the aquatic environment is a dynamic system with many interacting biotic and abiotic factors. The determination of limiting factors must therefore take into account the activity of the organisms as well as the water chemistry. The bioassay has become an important tool for determining the assimilation capacity of a receiving body of water.

Using the batch culture technique, an enrichment experiment was carried out to determine: 1) the assimilation capacity of the Spokane River at different points along its course, 2) the influence of urban discharges on algal productivity, and 3) whether phosphorus is a regulating factor in the river during the high and low flow periods.

Materials and Methods

Culture alga

A green form, *Selenastrum capricornutum* Printz, was selected for use in the algal bioassays. The selection of this alga was based on the following considerations: it is an obligate autotroph with a broad and noncomplex nutrient requirement; it occurs singularly and stays in free suspension, without lumping, with slight agitation; and

it has a distinct shape, uniform size, and occurs in oligotrophic and eutrophic waters. The culture of *S. capricornutum* was obtained from a common stock culture maintained by T. E. Maloney of the Pacific Northwest Water Laboratory, E.P.A., Corvallis, Oregon.

The basal nutrient used to maintain the culture was modified from the nutrient medium outlined by the Provisional Algal Assay Procedure (PAAP) (1969). The chemicals employed were of ultra-pure grade, with the exception of the potassium nitrate (KNO_3) which was reagent grade.

In inoculum preparation, a seven-day-old culture of *S. capricornutum* was centrifuged and the supernatant discarded. A portion of the sedimented cells was resuspended in PAAP medium deficient in phosphorus and cultured until cell density reached approximately 300,000 cells/ml. The cells were then acclimatized to filtered Spokane River water for five days, after which time they were resuspended in double distilled water so that when this suspension was added to the flask it resulted in an inoculum of 26,000 cells/ml.

Collection and analyses

Water samples from the Spokane River were collected by the Washington State Department of Ecology once during the months of June and August at the following stations (river mile): Sullivan Road Bridge (87.5) (control station—located several miles upstream of the city); Green Street Bridge (78.0), Fort Wright Bridge (69.8), Bowl and Pitcher (66.2) (all within the city proper—the latter located 100 yards below the primary sewage treatment plant); Long Lake (34.0), and Porcupine Bay Station #6 (12.8) (located 30 and 53 miles downstream, respectively). The samples were collected in five-gal polyethylene bags, packed in ice, and shipped immediately by air to the Sanitary Engineering laboratories at Washington State University. Water not used immediately was stored in the dark at 4°C. One-liter samples were also taken at each station and preserved with formalin for later algae identification and enumeration.

Nitrogen and phosphorus analyses were performed on the natural waters by the Washington State Department of Ecology, Olympia, Washington. Millipore-filtered water from the August samples was analyzed at the Washington State University laboratories for the trace metals copper, iron, zinc, and manganese using the Model 303 Perkin-Elmer Atomic Absorption Spectrophotometer.

Algal growth was measured by: 1) the microscopic cell count, using a compound microscope, at a magnification of 200X, in conjunction with an ocular Whipple disc and a Sedgewick-Rafter counting chamber, and 2) chlorophyll *a* absorbance, where absorbance was measured against a distilled water blank at 665 nm using a 5 cm path length in a Beckman DU Spectrophotometer.

Assay technique

Pyrex glass, 250 ml Erlenmeyer flasks were used for the oscillating batch cultures. The flasks were cleaned carefully according to PAAP, and 100 ml quantities of sample water (unfiltered and filtered) were transferred to three individual cotton-plugged flasks—one control flask and duplicate test (phosphorus) flasks. In the June assays indigenous algal populations in the test flasks were "spiked" with 1.0 mg P/1 and incubated until a stationary growth phase was reached. For the August assays growth studies were conducted with cultured algae replacing the naturally occurring species. In the laboratory the water samples were filtered through a .45 μ millipore mem-

brane to remove the planktonic organisms. Although some nutrients possibly may have been lost during the filtration process, the removal of all the planktonic organisms was necessary before incubation with the assay organism to prevent competition and predation. The 100 ml samples were inoculated with *Selenastrum capricornutum*, "spiked" with 0.1 mg P/1, and incubated until a stationary growth phase was reached.

Results and Discussion

Algal bioassays were conducted to determine the effects of phosphorus on the productivity of waters taken from the Spokane River during the late spring and summer of 1971. The experimental results of the June assays, using natural algal populations, are discussed in Part I. The August assays, using cultured algae, are discussed in Part II.

Part I—June analyses and assays

Six natural water samples from different stations along the Spokane River were collected for analysis and assaying with the bottle test. The algae composition of the river at the time of collection is shown in Table 1. Chemical analysis of the water for nitrogen and phosphorus compounds before and after filtration is shown in Table 2.

TABLE 1. Spokane River phytoplankton, June (August).

	Sullivan Rd.	Green St.	Cells/ml		Long Lake	Porcupine Bay
			Fr. Wright	Bowl & Pitcher		
Diatoms						
<i>Achnanthes</i> sp.	8 (24)	(52)	4 (92)	(84)		
<i>Asterionella</i> <i>formosa</i>	136	164	176	116	304	352
<i>Cyclotella</i> sp.	4		16	8	4	32
<i>Fragilaria</i> sp.	8 (160)	16 (112)	(128)	8 (180)	52 (32)	12 (240)
<i>Melosira italica</i>	1052	888	932 (24)	1068 (8)	2328	1652
<i>Navicula</i> sp.	44 (40)	24 (16)	60 (24)	48 (64)	28	32 (12)
<i>Surirella</i> sp.			8	12		
<i>Synedra</i> sp.	116 (12)	124 (16)	60 (28)	96 (24)	344 (4)	200 (92)
<i>Tabellaria</i> sp.	16	8	20 (4)	20		16
Miscellaneous		(4)	16	8 (8)		
Greens						
<i>Ankistrodesmus</i> sp.	144	116 (8)	12		152 (4)	24 (4)
<i>Chlamydomonas</i> sp.			(20)	4		4 (16)
<i>Coelastrum</i> sp.					(4)	
<i>Cosmarium</i> sp.	(8)					
<i>Dinobryon</i> sp.		4	8		8	
<i>Genicularia</i> sp.					(4)	(8)
<i>Gloeocystis</i> sp.					(24)	(12)
<i>Phacus</i> sp.	(4)			(8)	(100)	(8)
<i>Scenedesmus</i> sp.	24		48	16 (8)	20 (16)	32 (8)
<i>Sphaerocystis</i> sp.					(100)	(164)
<i>Tribonema</i> sp.	304	224	212	88	232	1232
Unknown	48	20			92	36
Miscellaneous	(4)	(4)	4		(8)	16 (24)
Blue-greens						
* <i>Apphanizomenon</i> <i>flos-aquae</i>	(62)	(60)	(18)	(2)		
* <i>Nostoc</i> sp.	(28)	(16)	(16)	(10)		
* <i>Oscillatoria</i> sp.				(6)		
TOTALS	1904 (342)	1588 (288)	1576 (354)	1492 (402)	3564 (300)	3640 (572)

* Standard units: filaments 100 μ long.

TABLE 2. Nitrogen and phosphorus chemical analysis.

Station (River Mile)	NH ₃ -N	Unfiltered			June (August) mg/l		Filtered Total-P	Ortho-P
		Kjeldahl-N	Total-P	Ortho-P	NO ₃ -N	Ortho-P		
Sullivan Rd. (87.5)	0(0)	.02(.14)	.016(.07)	.008(.02)	.01(.09)	.008(.04)	.008(.01)	
Green St. (78.0)	0(0)	.02(.28)	.028(.06)	.022(.01)	.03(.46)	.014(.07)	.006(<.01)	
Fort Wright (69.9)	0(0)	.02(.18)	.026(.06)	.018(.02)	.10(.58)	.026(.06)	.004(<.01)	
Bowl and Pitcher (66.2)	.02(.18)	.10(.14)	.032(.16)	.026(.07)	.09(.39)	.032(.10)	.022(.05)	
Long Lake (34.0)	—(.02)	.10(.24)	.028(.18)	.016(.06)	.05(.55)	.028(.18)	.002(.04)	
Porcupine Bay (12.8)	—(0)	—(.16)	.030(.14)	.010(<.01)	.11(.07)	.030(.12)	.010(0)	

Inspection of Table 2 shows an increase in nutrient levels as the river progresses through the city of Spokane toward its confluence with the Columbia River. Kjeldahl-nitrogen, nitrate-nitrogen, and phosphorus concentrations increase from Sullivan Road Bridge, reaching peak levels at the Bowl and Pitcher Bridge. Long Lake waters show a decrease in these chemical parameters, especially in the filtrate nitrate-nitrogen and orthophosphate. A good share of these compounds are probably tied up in the large biomass. It is also recognized that bottom sediments in lakes or reservoirs are efficient traps for certain nutrients (*i.e.*, iron, manganese, and phosphorus) under aerobic conditions. Dissolved orthophosphate may also be removed by excess absorption by green algae (Azad *et al.*, 1970), by diatoms along with silica (Schelske, 1971), and/or absorption by suspended particular matter. Nutrients consolidated into bottom sediments may be released slowly under anaerobic conditions. Bacterial activity also may play an important role in nutrient availability (other than organic degradation). Micro-organisms have been reported to solubilize "insoluble" inorganic phosphates (Gahler, 1969). To what extent these removal and release mechanisms influence phosphorus availability to algal cells in early growth stages is not known.

In contrast to the nutrient levels, algae productivity decreased from Sullivan Road Bridge to Long Lake, where the biomass more than doubled. Regardless of the relative decrease in cell numbers, the total phytoplankton production in the river was of "bloom" proportions. The diatoms made up the major portion of the algal population—the predominant species being the filamentous diatom *Melosira italica*. Two additional diatoms, *Asterionella formosa* and *Synedra* sp., were also prevalent, especially in Long Lake and Porcupine Bay. The latter station also supported an abundant population of *Tribonema* sp.—a yellow-green filamentous algae often associated with *Melosira* sp.

Oscillating batch assays were conducted to determine the effect of phosphorus on the indigenous algal species. Due to the difficulties involved in obtaining adequate cell mass estimates in low nutrient waters, the only usable parameter of growth was the cell count. To provide a measure of growth response to the phosphorus additions, mass growth rates (cells produced per day per total cells) were determined using

the method outlined by Krauss and Thomas (1954) and are presented graphically in Figure 1. Additional aids used in determining growth response were total yields (cell numbers), maximum growth rates (MGR), and the percentage increase in MGR (Table 3). It should be cautioned that the rates were based on a mixed algae culture and, therefore, are valid parameters only for this particular algal population and water mass. Growth response will show seasonal variations, depending upon climatic conditions and nutrient availability.

In the waters studied, the addition of 1.0 mg P/l resulted in a definite stimulation of the algal growth rates at all stations, except Bowl and Pitcher where there was a negative response (Fig. 1). This phenomenon is understandable since the filtrate waters already contained substantial concentrations of dissolved orthophosphate.

TABLE 3. Maximum growth rates (MGR).

Station	Maximum W/O P ^a	Cell No. With P	MGR (day ⁻¹) W/O P	MGR (day ⁻¹) With P	% MGR ^b
Sullivan Road	5,900	6,100	.48	.74	54
Green Street	10,100	10,800	.75	1.11	48
Fort Wright Street	12,700	18,850	.79	1.01	(120) ^c 28 ^d
Bowl and Pitcher	16,600	13,200	1.45	1.07	-45
Long Lake	16,900	19,000	.55	.80	44
Porcupine Bay	8,000	30,000	.48	.64	33

^a W/O P = without phosphorus.

^b MGR = percentage increase in maximum growth rate in the "spiked" flask over that in the control flask.

^c Based on growth rates of .42 (control) and .92 (test flasks) after 48 hours.

^d MGR after 96 hours.

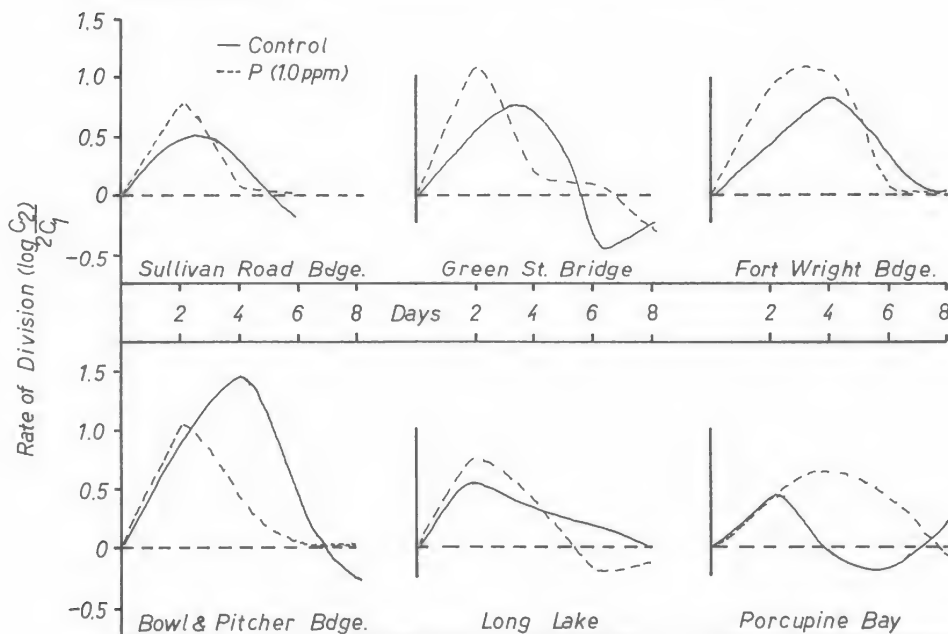


Figure 1. Effects of phosphorus on algae growth rates, June 15, 1971.

A slow response in the Porcupine Bay cultures suggests some phosphorus inhibition. After the second day, however, the algae population in one of the test cultures (the duplicate culture had severe grazing problems) finally responded to the phosphorus additions, resulting in the highest yield of the series. The green algae *Ankistrodesmus falcatus* was responsible for much of this increase.

The most immediate response to phosphorus additions came from the Fort Wright water, while the Sullivan Road sample produced the largest percent increase in maximum growth rate. With the exception of Porcupine Bay, phosphorus additions did not greatly increase total yields. Taken from the controls, these latter figures indicate the relative quantity of algae these particular waters are capable of supporting should no factor other than nutrients limit growth.

The results of this bioassay demonstrate that phosphorus additions to the river water (except at the Bowl and Pitcher station) could stimulate algal growth. Total productivity at each station, however, was controlled by additional factors, for the phosphorus "spiked" water did not produce total yields much greater than those in the control water, especially in the low-nutrient waters. Although phosphorus was apparently limiting in the major portion of the river, sufficient quantities of it and other growth-promoting factors must have been present earlier in order to support the current algal population. Therefore the phosphorus was only limiting after the fact—most of the nutrient was already tied up in a large biomass. Nutrient contributions from seasonal runoff and wastewater effluents only compounded the problem in Long Lake, where a longer residence time, warmer water, and nutrient recycling provided ideal growth conditions for an algal bloom.

Part II—August analyses and assays

The phytoplankton composition of the river at the time of the bioassay is presented in Table 1. Algal production was much lower than in late spring. Again the diatoms were the dominant algal group in the upper river; *Fragilaria* sp. being the most common form. The Sullivan Road and Green Street stations supported a relatively large population of the filamentous blue-green alga *Aphanizomenon flos-aquae*. The lower river stations supported an abundant green algae population, this group becoming the dominant form in Long Lake. The green euglenoid *Phacus* sp. and the green colonial *Sphaecocystis* sp. together made up two-thirds of the lake phytoplankton population.

The nutrient concentrations supporting these algal populations are shown in Table 2 (nitrogen and phosphorus) and Table 4 (micronutrients). In general nitrogen and phosphorus compounds were in higher concentrations during the August sampling period. Much of this increase was likely due to the concentration effect of low river

TABLE 4. Micronutrient analyses by atomic absorption, August 1971 (filtered).

Station	mg/l			
	Cu	Mn	Zn	Fe
Sullivan Road	<0.002	0.001	0.098	<.004
Green Street	0.006	0.002	0.098	<.014
Fort Wright	<0.002	0.005	0.052	0.010
Bowl and Pitcher	0.006	0.009	0.118	0.010
Long Lake	0.004	<.001	0.046	0.004
Porcupine Bay	0.006	<.001	0.024	<.004

flow. The orthophosphates show little change from June in the first three stations, but rise significantly at the Bowl and Pitcher Bridge. Total-phosphorus and ammonia-nitrogen also rise abruptly at this station, indicating a substantial contribution of these nutrients from the wastewater treatment plant. Kjeldahl-nitrogen and nitrate-nitrogen are at high levels throughout the river, with the exception of the latter at Sullivan Road and Porcupine Bay.

With the high nitrogen and phosphorus levels present one might wonder why the river does not support a large algal population similar to the one in June. The June population was a "seasonal" bloom resulting from warming temperatures and a greater influx of essential growth elements from higher surface runoff. Several inorganic elements are required in relatively large concentrations for growth and reproduction of all algae. These "macronutrients" are carbon, oxygen, hydrogen, nitrogen, sulfur, phosphorus, iron, calcium, and magnesium (Eyster, 1964). Minute quantities of other inorganic elements (micronutrients) are also utilized in algae nutrition. Included are the metallic constituents of enzymes and co-enzymes (copper, manganese, molybdenum, and zinc) and chlorine which is involved with oxygen revolution during photosynthesis (Eyster, 1964, 1968; O'Kelley, 1968). Other micronutrients such as boron, cobalt, iodine, silica, sodium, and vanadium are essential to the nutrition of some but not all species of algae (Eyster, 1964, 1968; O'Kelley, 1968; Wiessner, 1962). Other factors that influence algal growth are vitamins, other trace metals, hormones and auxins, extracellular metabolites, autointoxicants, viruses, and predation and grazing by aquatic animals (Mackenthun, 1969).

Some of the latter factors may be of equal importance to the major nutrients in influencing algal production. Many of the trace elements and vitamins are primarily supplied in small quantities from natural sources. Low runoff can greatly influence the optimal concentrations and availability of many of these trace elements. Metal chelators (such as NTA [nitrilotriacetic acid]) or naturally occurring humic substances may also increase or decrease the availability of essential trace nutrients (Erickson, Lackie, and Maloney, 1970; Shapiro, 1964). Bacterial degradation of NTA can also supply additional nitrogen for algal assimilation (Erickson, Maloney, and Gentile, 1970).

Low flow conditions in the river may concentrate potentially inhibiting metals and/or organic compounds contributed by industrial or domestic wastewater. The toxicity of a particular substance is species-dependent and is influenced to a large degree on the water chemistry associated with the toxicant, such as temperature, pH, alkalinity, etc. (Mackenthun, 1969). Many of the metals interact in a synergistic or antagonistic manner to promote or retard algal growth directly, or indirectly by affecting predators (Jones, 1964).

Zinc concentrations in the river (.024-.118 mg Zn/l) were at levels far above what is essential for algal growth. Optimal concentrations of zinc for algal growth as low as .001 mg Zn/l have been reported (Eyster, 1968). Concentrations of copper in the river were found to be in the range of .002-.006 mg Cu/l. Photosynthesis in the green algal form, *Chlorella vulgaris*, has been reported to be inhibited by .0064 mg Cu/l (Greenfield, 1942).

To determine the effects of phosphorus on the algal growth rates and assimilation capacity of the natural waters, oscillating assays, using a cultured alga in place of

the natural algal population, were conducted on filtered river water. Surface waters from six stations along the Spokane River were filtered through a millipore membrane and inoculated with the green algae, *Selenastrum capricornutum*.

After a two-day acclimation period, the cultures were "spiked" with 0.1 mg P/l, and incubated over a 13-day period (Figs. 2-7). Growth response was determined by absorbance. (Approximate cell concentrations can be determined by using the conversion curve presented in Figure 8.)

The relative productivity and growth parameters of the six waters under controlled experimental conditions are summarized in Table 5.

The experimental results indicate that productivity was governed by factors other than limiting concentrations of phosphorus. At all stations phosphorus additions produced a slight to pronounced inhibition to algal growth. While the lack of en-

TABLE 5. Growth parameters in the control flasks.

Station	Av. Growth Rate ^a over 1st 7 days	Maximum Absorbance	Av. Max. Cell No. (cells/ml)	Days to M.A.
Sullivan Road	.32 ^b	.052	80,000	6
Green Street	.27	.060	100,000	5
Fort Wright	.45	.196	315,000	11
Bowl and Pitcher	.49	.254	410,000	11
Long Lake	.54	.253	405,000	11
Porcupine Bay	.33	.081	130,000	7

^a In units of day⁻¹.

^b Based on a five-day average.

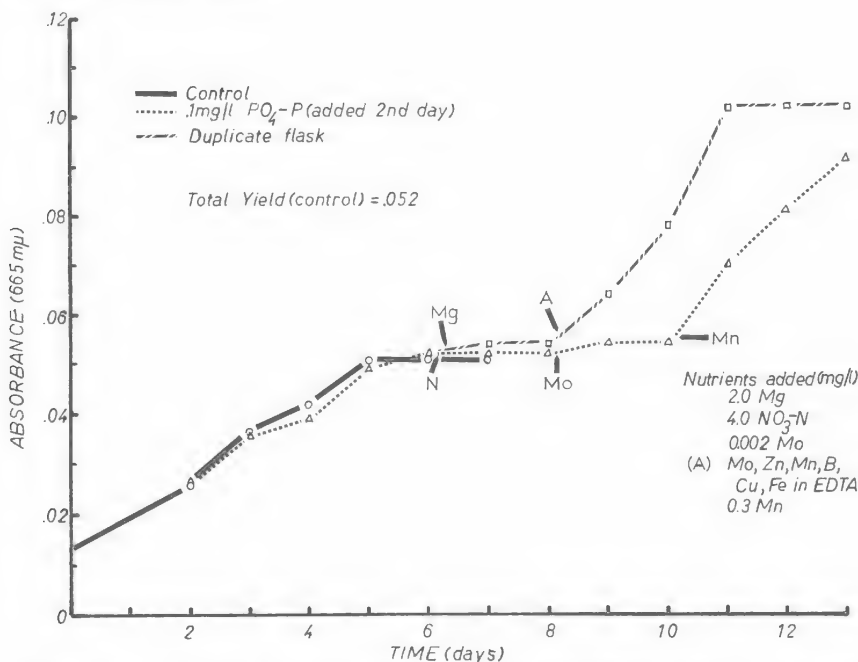


Figure 2. Effects of $\text{PO}_4\text{-P}$ and other nutrients on *S. capricornutum* growth, Sullivan Road, Spokane River, August 17, 1971.

hancement can be attributed to sufficient concentrations of phosphorus in the water, the inhibition by phosphorus can only be postulated. The maximum growth rate of the algae is determined by the set environmental conditions, these being light, temperature, cell density, and nutrient concentrations. When inorganic phosphorus is already present beyond the usual metabolic requirements of the cell, the nutrient is absorbed

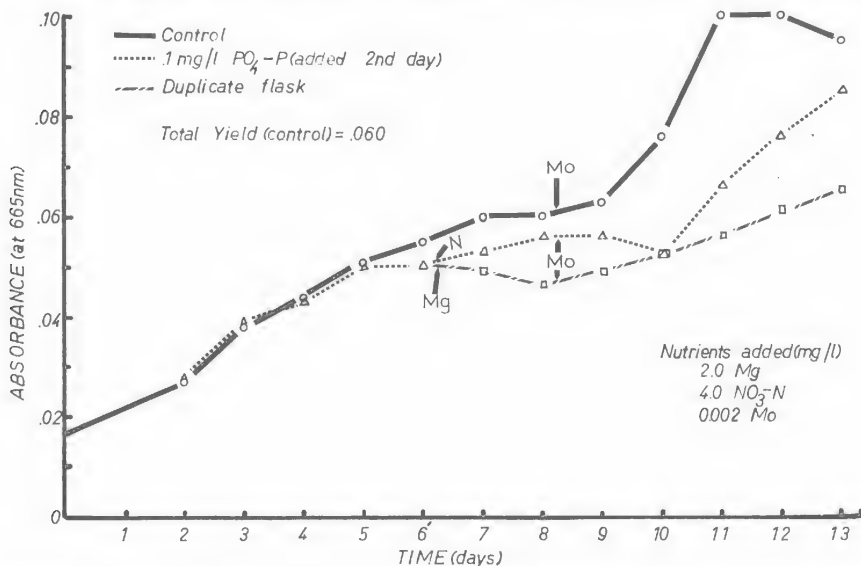


Figure 3. Effects of $\text{PO}_4\text{-P}$ and other nutrients on *S. capricornutum* growth, Green Street, Spokane River, August 17, 1971.

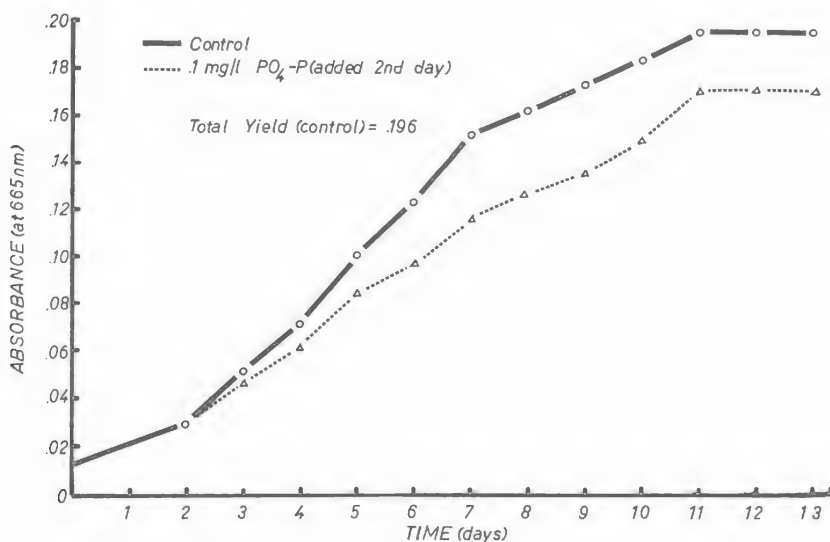


Figure 4. Effect of $\text{PO}_4\text{-P}$ on *S. capricornutum* growth, Fort Wright Road, Spokane River, August 17, 1971.

and stored in excess quantities (Azad *et al.*, 1970). The increased levels of phosphorus in the algal cells may repress the biosynthesis of enzymes responsible for the P-uptake reactions—in turn reducing the net transport of phosphorus from the medium. Addition of phosphorus may change the interaction kinetics of the chemical constituents, thereby affecting the availability of other nutrients for assimilation by

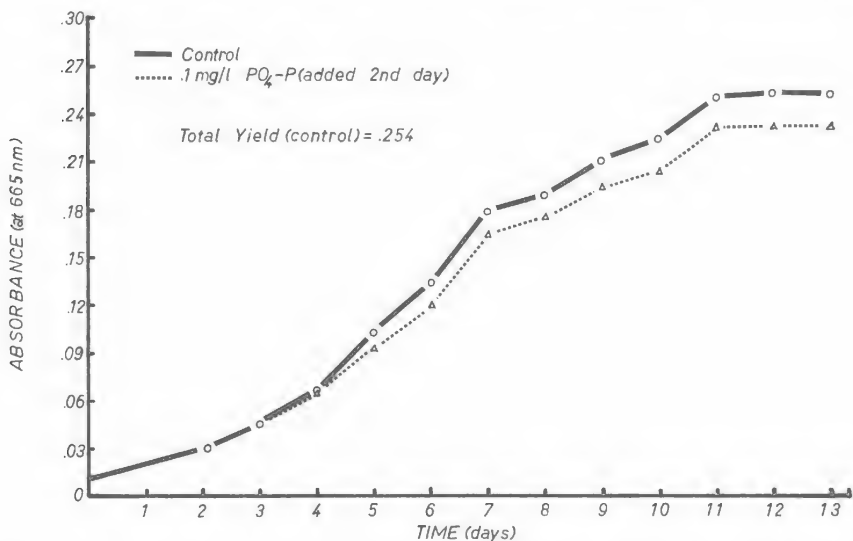


Figure 5. Effect of $\text{PO}_4\text{-P}$ on *S. capricornutum* growth, Bowl and Pitcher Road, Spokane River, August 17, 1971.

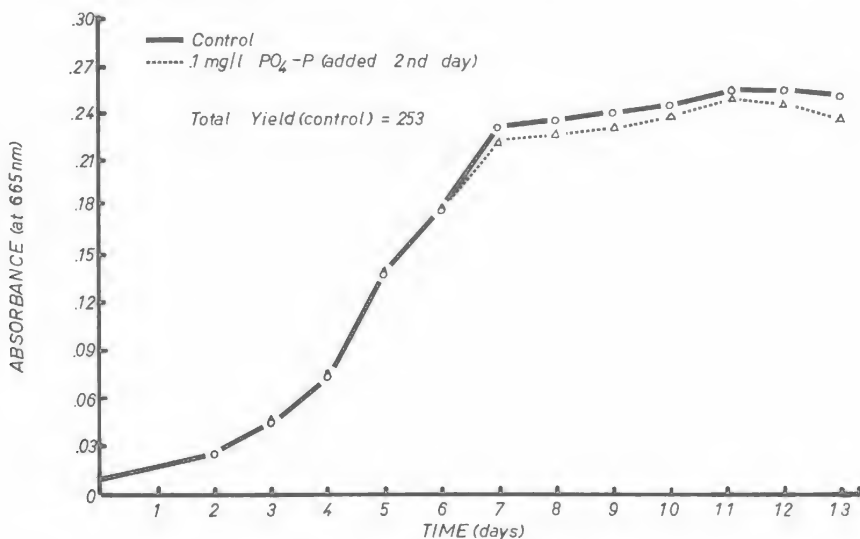


Figure 6. Effect of $\text{PO}_4\text{-P}$ on *S. capricornutum* growth, Long Lake, Spokane River, August 17, 1971.

the algal cells. The end result could mean a stimulation or repression of algal growth, the latter being indicated in this case.

An attempt was made to determine whether the factor(s) limiting the growth

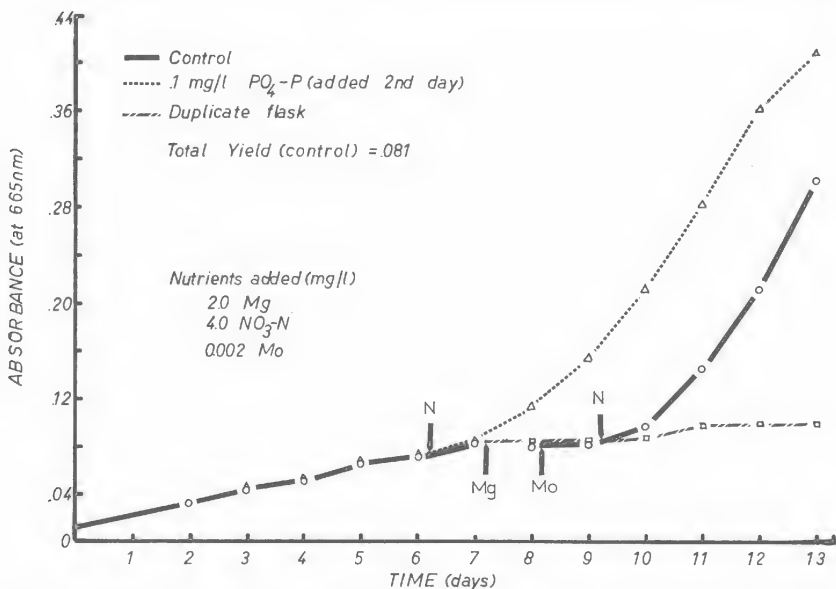


Figure 7. Effects of $PO_4\text{-P}$ on $NO_3\text{-N}$ on *S. capricornutum* growth, Porcupine Bay, Spokane River, August 17, 1971.

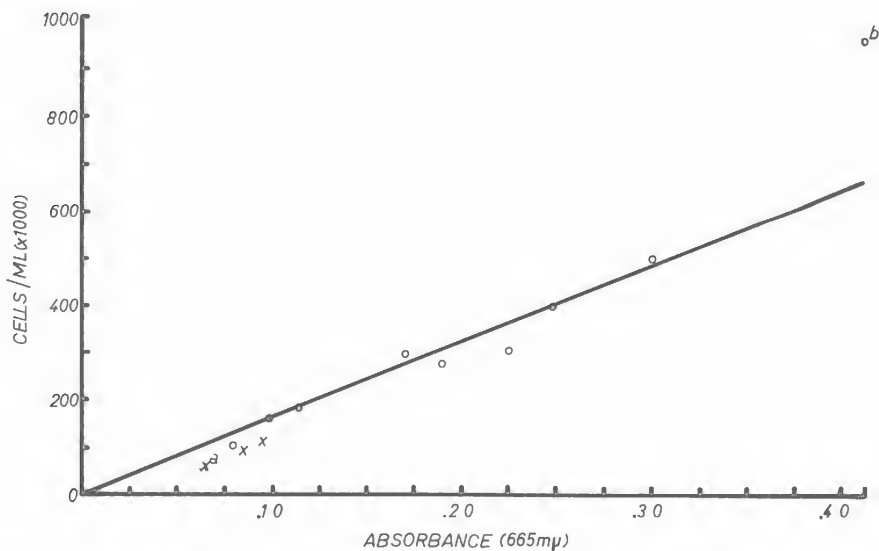


Figure 8. Relationship between chlorophyll *a* and *Selenastrum capricornutum* cell no.

^a Effect of molybdenum on the Green Street cultures.

^b Effect of nitrogen on cell number/absorbance ratio.

in the low-yield waters was a major or trace nutrient. The macronutrients magnesium (as MgSO_4) and nitrogen (as KNO_3) were added separately to the test flasks of the Sullivan Road, Green Street, and Porcupine Bay samples (Figs. 2, 3, 7). The magnesium additions produced no positive response in any of the waters. Nitrate-N, on the other hand, greatly stimulated algal growth in the Porcupine Bay water. The effect on cell division was so pronounced that cell numbers and chlorophyll production no longer correlated. Nitrogen concentrations beyond an optimal range have been found to inhibit the formation of chlorophyll in green algae (Mackenthun, 1969). The extremely high cell number/absorbance ratio shown in Figure 8 supports this observation. The average algal growth rate was raised from 0.0 day^{-1} to 0.44 day^{-1} in the test flask. The nitrogen was then added to the control flask as a double check for phosphorus availability. The average growth rate increased from 0.0 day^{-1} to 0.47 day^{-1} , reinforcing the earlier conclusion that phosphorus was not limiting.

At this point the micronutrient molybdenum was added to one of the Sullivan Road test flasks and to all three Green Street flasks. This element had no effect on the test algae. The flasks in the Green Street sample, however, had become contaminated with the blue-green form *Aphanizomenon flos-aquae*. Molybdenum, necessary for nitrate utilization and nitrogen fixation (Arnon *et al.*, 1955; Eyster, 1959), stimulated the growth of this blue-green. The result was a higher absorbance in all three flasks than the number of *Selenastrum* cells could account for (Fig. 8). The difference in absorbance was due to the blue-green contamination.

The limiting factor in the Sullivan Road water was still unresolved. In an effort to determine which, if any, trace element(s) was limiting a test flask was "spiked" with a combined stock of several micronutrients (molybdenum, zinc, copper, manganese, boron, and iron in EDTA). Within 24 hours the growth rate was raised from 0.0 day^{-1} to 0.35 day^{-1} . The total yield was more than doubled in three days. One of the elements in the stock solution appeared to be limiting in the natural waters. Manganese, one of the key elements in photosynthesis, was selected as a likely candidate. Its addition to the other test flask resulted in an immediate stimulation of the algal growth rate from 0.0 day^{-1} to 0.26 day^{-1} .

Summary and Conclusions

The batch bottle assay using indigenous algal populations proved to be a simple and reliable method for determining the productivity of natural waters. The algal cultures responded to nutrient additions rapidly, with no "apparent" lag time. When properly acclimated the green algal form, *Selenastrum capricornutum*, proved to be an adequate and responsive test organism for natural water bioassays.

The growth parameters obtained from the control flasks indicate that during the test periods the total productivity and algal growth rates in the natural waters increase as the river progresses through the city.

During the spring months high runoff provided adequate nutrients to promote algal growth in bloom proportions. The large biomass reduced phosphorus concentrations to limiting levels in the river. The especially high algal production in the lower river was due in part to the added phosphorus contributions made by the wastewater treatment plant above the Bowl and Pitcher Bridge. Dissolved orthophosphate levels at this station were sufficiently high enough to cause inhibition to algal growth rates when additional phosphorus was introduced in the bioassay.

The August bioassay indicated that productivity was governed by factors other than limiting concentrations of phosphorus. Nitrogen was found to be limiting in Porcupine Bay, while manganese appeared to be a limiting factor in Sullivan Road waters.

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Experimental Infections with *Fasciola hepatica* from Eastern Washington and Northern California¹

The laboratory mouse is a suitable experimental host for *Fasciola hepatica* L. according to Dawes (1962), Dawes and Hughes (1964), Lang (1966, 1967, 1968a,b), and Boray (1963); however, great variation was reported in the size of the infecting dose, worm recovery, and mortality in mice. Studies by Shirai (1927), Taylor and Parfitt (1957), and Lagrange and Gutmann (1961) indicated that the laboratory mouse was not a suitable experimental host as a single parasite might result in death of the host. Apparently, the strain of mouse and parasite play a role in the suitability of any *Fasciola*-mouse system for experimental work.

Studies on the immunology and host-parasite relationships of *F. hepatica* in a single strain of mouse have demonstrated that this strain is suitable for studying certain host responses manifested against two-worm infections and that males develop acquired immunity following immunizing infection (Lang, 1966, 1967, 1968a,b; Lang *et al.*, 1967). This work used a strain of parasite from northern California alternately maintained in mice, rabbits, and occasionally rats in an attempt to avoid any immediate or long-term adaptation to the mouse host. The snail *Lymnaea columella* Say was utilized in all published studies; however utilizing *L. bulimoides* Lea had no detectable effect on host and parasite behavior following single two-worm infections (Lang, unpublished data).

The present study deals with the host responses and parasite growth and behavior of *Fasciola* from eastern Washington. Before immunological studies on the *Fasciola*-mouse system could be continued using a parasite from a different area, the host responses manifested against this parasite and parasite behavior had to be determined.

Materials and Methods

Mice utilized were from an isologous strain maintained in the Department of Parasitology, University of North Carolina. Techniques for infection and necropsy of mice, handling of recovered worms, determination of host responses, and infection of snail hosts have been described (Lang, 1966). Tissues were processed using an International Cryostat.

Eggs of *Fasciola* from eastern Washington were obtained from infected cattle, while eggs from California were obtained from laboratory-infected rabbits. Eggs were embryonated and one- to four-week-old laboratory-raised *L. bulimoides* were exposed to miracidia. Twenty-four hours after exposure, snails were transferred to clay pots (22 cm by 5 cm) containing food and filtered spring water. Sixty days after exposure snails were isolated in jars for collection of metacercariae which were stored at 13°C. Worm measurements are in millimeters, the mean followed by the range.

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Experimental Procedures and Results

To determine baseline data on *Fasciola* from eastern Washington, 56 male mice with an average weight of 31.5 g at infection (18 to 20 weeks old) were divided into two groups of 36 (Group I, Washington) and 20 (Group II, California) and each mouse was given two metacercariae (40 to 80 days old). Body weights were taken the day of infection, 7, 14, 18, 22, 25, 27, 31, 35, 42, and 49 days after infection. Four mice from each group were used for differential leukocyte determinations at the above intervals. Group III (uninfected controls), 12 mice, provided normal body weights and differential counts. For Group I, eight mice were necropsied at 10, 12, 17, 19, 24, 33, 35, and 40 days post-infection for worm recovery and tissue for histopathology. Remaining mice were necropsied 50 days post-infection. Group II mice were necropsied at corresponding times after 19 days of infection and at selected mortality times for Group I. Thus, for Group II 16 mice were necropsied at 24, 30, 32, 40, and 50 days post-infection. No tissues for histopathology were taken from this group as tissue responses for this system are well documented (Lang, 1966, 1967). Recovered worms from both groups were measured at selected times after infection.

All mice exposed to metacercariae were infected. For Group I, 90.3 percent (65/72) of the worms were recovered, while 90.0 percent (36/40) of the worms were recovered from mice of Group II. Group I mice began dying 25 days after infection. Between 25 and 33 days after infection 10 animals died (Table 1). Five animals had been necropsied prior to the onset of mortality, thus they were not mortality risks. Mortality in Group I was 32.3 percent (10/31). Group II mice began dying 26 days after infection. Between 26 and 28 days, four mice died. Two animals had been necropsied prior to the onset of mortality. Mortality in Group II was 22.2 percent (4/18).

TABLE 1. Worm recovery and location of worms from mice infected with two *Fasciola hepatica* metacercariae each at intervals after infection.

Days after infection	Number of Mice Group I	Group II	Location and Condition Group I	Group II
10-19	4(8) ¹	0	LP-I ²	—
24	1(2)	2(3)	LP-I	LP-I
25	4*(7)	0	LP-I	—
26	2*(3)	1*(2)	LP-I	LP-I
27	1*(1)	2*(4)	LP-I	LP-I
28	0	1*(2)	—	LP-I
29	1*(2)	0	LP-I	—
30	1*(2)	2(4)	LP-I	LP-I
32	1*(2)	2(4)	BD-I ³	LP-I
33	1(1)	2(4)	BD-M ⁴	LP-I
35	1(2)	2(4)	BD-M	BD-I
40	1(1)	2(3)	BD-M	BD-M
50	18(34)	4(6)	BD-M	BD-M
Totals	36(65)	20(36)		

¹ Number of worms recovered ().

² Liver parenchyma, immature.

³ Common bile duct, immature.

⁴ Common bile duct, mature.

* Animal(s) died.

As shown in Table 1, worms were located in the liver parenchyma of mice from both groups until 30 days after infection. In Group I, immature worms were recovered from the common bile duct by 32 days post-infection, while immature worms from Group II were not recovered from the common bile duct until 35 days post-infection. Worms of Group I were producing few eggs by 33 days after infection and numerous eggs by 35 days after infection, while worms of Group II did not produce eggs until 40 days after infection and then only a few. By 50 days these worms were producing numerous eggs.

Prior to movement into the common bile ducts worms of Group I were slightly larger than those of Group II. Group I: 24 days, 4.4 (4.3 to 4.5); 26 days, 4.8 (4.6 to 5.0); 30 days, 6.1 (5.9 to 6.3); 32 days, 6.8 (6.7 to 6.9); 35 days, 7.2 (7.0 to 7.4); 40 days, 12.6 (12.6); 50 days, 13.8 (13.5 to 14.3). Group II: 24 days, 3.6 (3.3 to 4.0); 26 days, 4.2 (4.0 to 4.4); 30 days, 5.4 (4.9 to 5.7); 32 days, 6.7 (6.4 to 6.9); 35 days, 8.8 (8.2 to 9.4); 40 days, 12.7 (12.4 to 13.0); 50 days, 12.9 (12.4 to 13.0). In both groups, after the worms reached the common bile duct and began to produce eggs, there was a decrease in growth rate. This was more marked in worms of Group II.

Host responses for mice of both groups were very similar. Between 18 and 25 days after infection mice from Group I lost an average of 2.5 g per animal while mice from Group II lost an average of 2.0 g during the same interval. Both groups gained weight after 25 days with Group I mice averaging 33.1 g by 42 days after infection and Group II mice averaging 32.9 g at the same time. Group I mice gained weight somewhat more rapidly. Uninfected controls (Group III) showed steady weight gain throughout the experiment.

The differential leukocyte determinations for Group I indicated a reversal in the lymphocyte-neutrophil ratio from 22 to 35 days post-infection as compared to a corresponding reversal occurring 25 to 31 days post-infection in Group II. No reversal was observed in mice of Group III.

Host reaction to worm damage in the liver of Group I mice at 10 to 17 days post-infection was characterized by an inflammatory zone of polymorphonuclear leukocytes and necrotic hepatic cells around worm burrows. By 17 days after infection large areas of the parenchyma were necrotic and small lymphocytes were present throughout the liver. This pathology and that seen after 19 days of infection was almost identical with previous reports for this system (Lang, 1966, 1967).

Discussion

In comparing the two parasite populations it is apparent that differences in worm behavior are present. Worms of the Washington population migrated into the common bile duct sooner (three days), produced eggs earlier (seven days), and were larger prior to moving into the common bile duct and by 50 days after infection than worms of the California population. Also, mortality was higher (32.3 vs. 22.2 percent) in mice infected with worms from Washington. It was also observed that overall gross liver damage appeared more severe in these mice than seen in Group II and previous work (Lang, 1966).

The histopathological and weight course of the infections appears to be similar between the two populations, except that mice infected with worms from the California population did not appear to gain weight as rapidly after the acute phase of

infection. Slight differences were observed in the period of lymphocyte-neutrophil inversion. Mice of Group I had a longer reversal period (22 to 35 days post-infection) which was initiated three days sooner than in mice in Group II. It appears that the worms from the Washington population are slightly more pathogenic in the strain of mouse used than worms from the California population as seen in this study and others (Lang, 1966, 1967, 1968a).

With the above similarities in host responses and slight differences in parasite biology, it is felt that the experimental approach previously used in the mouse-*Fasciola* system and the data accumulated on host-parasite relationships and acquired immunity are applicable to this system using *F. hepatica* from Washington.

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Seasonal Variations in Forest Birds of Western Oregon

Introduction

The western part of Willamette Valley, Oregon grades from an open savannah-like area into dense Oregon white oak (*Quercus garryana*) woods which probably originally developed there following settlement by white man, who prevented the brush fires which previously maintained the oaks in an open savannah. The increased shade from dense canopy in such woods prevents oak seedlings from growing, allowing Douglas-fir (*Pseudotsuga menziesii*) to germinate under the oak canopy in dry areas. In moist areas near streams, washes, and north-facing slopes, big leaf maple (*Acer macrophyllum*) develops, and grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), or western red cedar (*Thuja plicata*) follow Douglas-fir in succession depending on altitude and exposure.

Within the three major vegetative types oak-fir-hemlock, I sought to characterize the seasonal changes in bird species composition, diversity, and ecological structure. Ten study areas were used. A permanent transect was established with a surveyor's tape in each area so that the same portion could be censused for avifauna composition on each visit. The areas varied from a pure oak stand through the Douglas-fir sere into the western hemlock sere.

Methods

To record and compare the avifaunal composition of several sample plots, a method was sought which would give a relative abundance index rather than an absolute population count. Four methods were selected for analysis: the strip census, the strip map, the point quarter, and the sample count. Each method was used in the same 120-acre stand of Oregon white oak located on the north-facing slope of Pigeon Butte, 12 mi south of Corvallis, Oregon (T13S, R5W, Sec. 31, N.E.-¼) in the spring of 1967.

Care was taken to conduct all censuses under similar conditions. Thus, all censuses were made between 0600 and 0900 on sunny, calm mornings. The results of censusing which began on May 15 and continued through June 4 were recorded in Table 1. Periodic censuses were made during the fall and winter. The following spring, the procedure was repeated in several conifer stands to see if the method selected could be used in all stands on an annual basis.

All birds seen in the vegetation were counted. When a singing bird was heard, an attempt was made to see if it was within the census area. If so, it was counted only if visually observed. When a presumed singing male was found, an attempt was made to locate the female. The female was not counted unless she was observed within the census area.

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TABLE 1. Comparison of four census methods.

Species	Strip Census	Census Method ¹		Sample Count
		Strip Map	Point Quarter	
Ring-necked Pheasant	1.6	0.0	0.0	0.0
Hairy Woodpecker	3.1	2.2	2.9	0.0
Downy Woodpecker	3.1	2.2	2.9	2.0
Western Wood Pewee	0.0	0.0	0.0	3.9
Black-capped Chickadee	4.7	8.9	5.9	7.8
Common Bushtit	6.3	6.7	5.9	5.9
White-breasted Nuthatch	3.1	4.4	5.9	3.9
Red-breasted Nuthatch	3.1	2.2	2.9	2.0
Brown Creeper	1.6	2.2	2.9	3.9
Bewick's Wren	0.0	4.4	2.9	3.9
Robin	9.4	4.4	5.9	5.9
Hutton's Vireo	0.0	2.2	2.9	2.0
Solitary Vireo	6.3	4.4	2.9	3.9
Warbling Vireo	3.1	2.2	2.9	3.9
Orange-crowned Warbler	12.5	11.1	8.8	7.8
Yellow Warbler	0.0	0.0	2.9	2.0
Audubon's Warbler	1.6	0.0	2.9	2.0
MacGillivray's Warbler	3.1	8.9	2.9	3.9
Wilson's Warbler	9.4	6.7	5.9	5.9
Western Tanager	3.1	4.4	2.9	3.9
House Finch	6.3	4.4	5.9	3.9
Rufous-sided Towhee	9.4	8.9	8.8	9.8
Oregon Junco	3.1	4.4	5.9	3.9
Chipping Sparrow	6.3	4.4	5.9	7.8
Species recorded	20	20	22	22

¹ Relative density of species.

The Strip Census Method. Using the strip census methods of Forbes and Gross (1923), five 120-ft wide strips were located parallel to one another, 500 ft apart. Each strip was 1000 ft long. The width of these strips was established on the basis of preliminary observations which indicated that I could see and flush birds up to 60 ft on each side of the strip. Beyond that distance, differences in the conspicuousness of individuals and species provided a source of bias. To census an area, I walked slowly along the center of the strip counting all birds seen within the 60 ft on either side.

The Strip Map Method. The second method used was an adaptation of the strip census method using a map of the region. A single transect 120 ft wide and 3000 ft long was established. This transect crossed the five strips used in the strip census method at right angles. Important topographic and vegetative features were marked on the map, which was duplicated and used to record the location of all birds seen as I walked down the center of the mapped rectangle.

The Point Quarter Method. Using this method, which was originally proposed for phytosociological sampling by Cottam and Curtis (1956), 10 points were selected by means of a random numbers table along the same 3000-ft transect used in the strip map method. The space around each point was divided into four quarters by bisecting the transect at a 90° angle. As I could observe birds for a distance of 60 ft in all directions, each quarter consisted of one-fourth of a circle with a 60-ft radius. When I reached a point, the first bird seen in a tree, on a shrub, and on the ground in each quarter was recorded; sometimes no bird was seen in one or more of these positions. Birds heard were not recorded unless they moved into view.

The Sample Count Method. This method was first used for bird population studies by Bond (1957). In my study, I established 10 observation points at intervals of 312 ft along a transect through the stand. As I walked through the stand, I stopped at each sample point for 10 minutes and recorded all birds seen within 60 ft of the point. Following the 10-minute stop, I walked slowly to the next point, recording all birds seen within 60 ft on either side of the transect.

In Table 1, the relative density for each species was calculated by dividing the number of individuals of that species by the total number of individuals seen. Three censuses were made of the stand with each of the methods, and the largest number of individuals per species recorded during these three times was considered as the local population of the species. As this was the breeding season, nomadic wandering of groups of birds was at a minimum.

The minimum time required for each method was as follows: strip census—three hours; strip map—two and a half hours; point quarter—two and a quarter hours; sample count—three hours.

The largest number of individuals was observed when the sample count method was used. This was probably an outcome of the 10-minute waiting period made at each stop. Some species were inevitably disturbed when an observer moved through heavy understory. Some birds such as the warblers, vireos, and chickadees may stop their activity or leave the area. Other species like the Rufous-sided Towhee (*Pipilo erythrophthalmus*) may be flushed by the approaching observer. In general, the different methods recorded similar numbers of species, although the sample count and quarter methods listed two more species than the strip map and strip census methods.

Twenty-one species were recorded in common by the sample count and quarter methods. This was the largest number of species shared by any two methods. The largest number of individuals was observed using the sample count method and the fewest with the quarter. Both methods thus appeared equally sensitive to the species composition of the stand, although the quarter method, because it recorded only the first bird seen in a particular stratum, underestimated the density of individuals in strata of great concentration and overestimated the population in strata of smaller concentrations of birds. The quarter method was founded on the assumption of random distribution of individuals in the community sampled (Cottam and Curtis, 1956). Birds are known not to be randomly distributed because of behavioral and environmental interactions. When one confines his study to a limited area such as an oak stand, a random census method such as the quarter method therefore would be expected to give an inaccurate representation of the avifaunal composition; that the method measured the species composition so well was surprising.

While using the strip census method, it was felt that many birds were being counted more than once as they flew across the strips and the observer walked back and forth. Utilizing the strip map, quarter, and sample count methods, it was felt that this duplicate counting was reduced. It was often possible to keep track of the birds as one moved along the transect. This, however, was not accurate and duplicate counting remained a problem with all of the methods.

Both the sample count and the quarter methods indicated the largest number of species present; however, the sample count showed a considerably larger total number of birds present. Time-wise, the sample count took a little longer; however, the total

picture of the avian population appeared more accurate. Thus, the sample count method was adopted for this study. Continued analysis of the sample count method yielded similar results in all forest types throughout the year.

The Study Areas

The 10 study areas used in this study were located on the eastern slope of the coast range (Table 2). A permanent transect was established in each area and censuses were conducted at least once a month between January 1968 and January 1970. All morning censuses were begun one hour after sunrise. Evening censuses were made once each season beginning one hour prior to sunset. During the breeding season (April to August), avian population fluctuated greatly so weekly censuses were made in each study area.

The study sites were divided into the three vegetative types as follows: areas one and two, Oregon white oak with a dense understory of poison oak (*Rhus diversiloba*); areas three through eight, Douglas-fir with Oregon grape (*Berberis aquifolium*), bracken fern (*Pteridium aquilinum*), and many other shrubs.

Results

Typically, avifaunal activity followed different seasons than the four-season calendar. Food supply, nesting material, climate, cover sites, and other factors contributed to changing avifaunal composition and activity. Twomey (1954), in a study of the elm-maple forests in central Illinois, recognized six avifaunal seasons. Anderson (1970) found that the birds of Oregon white oak habitats followed a seasonal pattern similar to the birds of the elm-maple community. They were:

Winter	November 2 through March 1
Early Spring	March 2 through April 15
Late Spring	April 16 through June 1
Early Summer	June 2 through July 15
Late Summer	July 16 through September 1
Fall	September 2 through November 1

The birds of the Douglas-fir and western hemlock communities followed the same seasonal patterns as did the birds in Oregon white oak stands. This study, therefore, was conducted within the framework of these six seasons (Tables 3, 4 and 5).

Bird species were classified as permanent residents, summer residents, winter resi-

TABLE 2. Features of the study areas.

Area Number	Size in Acres	Location	Exposure	Trees per Acre	Height Class Distribution			Percent Canopy Cover
					<30'	30-60'	>60'	
1	120	T13S, R5W, Sec. 31, NE $\frac{1}{4}$	N	110	16	39	45	82
2	125	T10S, R5W, Sec. 27, SE $\frac{1}{4}$	E	117	42	37	20	72
3	105	T11S, R5W, Sec. 9, NW $\frac{1}{4}$	E	90		15	85	61
4	200	T11S, R5W, Sec. 7, SW $\frac{1}{4}$	N	115	3	9	88	86
5	140	T11S, R5W, Sec. 8, SW $\frac{1}{4}$	W	60	5	10	85	89
6	90	T12S, R7W, Sec. 15, NW $\frac{1}{4}$	S	172	2	4	94	98
7	125	T12S, R7W, Sec. 10, SE $\frac{1}{4}$	E	65		7	93	64
8	140	T11S, R5W, Sec. 8, SE $\frac{1}{4}$	N	54		10	90	89
9	110	T12S, R7W, Sec. 16, NW $\frac{1}{4}$	N	152	2	8	90	72
10	115	T12S, R7W, Sec. 9, SE $\frac{1}{4}$	W	164	4	8	88	78

dents, and occasional visitors, based on the time spent in the community and the type of occupancy. Some species were classified differently in different communities. Permanent residents were observed during all seasons and were either directly observed nesting or presumed to be nesting on the basis of indirect evidence (*e.g.*, territorial

TABLE 3. Population census results for avifauna of Oregon white oak.¹

Species	(Resident Type) ²	Season					
		Winter	Early Spring	Late Spring	Early Summer	Late Summer	Fall
Turkey Vulture	(O)		22	11	33	22	22
Red-tailed Hawk	(O)	11	22	11	11	11	11
Ring-necked Pheasant	(O)	22	11				
Band-tailed Pigeon	(O)				66	22	55
Great Horned Owl	(O)			1			
Rufous Hummingbird	(S)				11		
Red-shafted Flicker	(O)		44		22		
Pileated Woodpecker	(O)				2		
Yellow-bellied Sapsucker	(O)	11					
Hairy Woodpecker	(P)	11	22	22	11	11	11
Downy Woodpecker	(P)	11	22	22	22	11	11
Western Wood Pewee	(S)		11	22	22	22	22
Steller's Jay	(W)	33					
Scrub Jay	(P)			11			
Crow	(O)		11				
Black-capped Chickadee	(P)	132	110	110	110	154	198
Common Bushtit	(P)	33	22	44	44	22	33
White-breasted Nuthatch	(P)	44	66	44	88	88	44
Red-breasted Nuthatch	(W)	22					
Brown Creeper	(P)	44	66	44	66	66	22
Winter Wren	(W)	11	11				
Bewick's Wren	(P)	11		22	22	11	
Robin	(P)	22	22	88	66	11	11
Varied Thrush	(W)	33	33				
Hermit Thrush	(S)			11	22		
Western Bluebird	(O)	33					
Townsend's Solitaire	(O)		11				
Golden-crowned Kinglet	(W)	22	77				66
Ruby-crowned Kinglet	(W)	33					
Cedar Waxwing	(O)	33					
Hutton's Vireo	(P)	11	22	22	22		11
Solitary Vireo	(S)			22	33		
Warbling Vireo	(S)			22	22		
Orange-crowned Warbler	(S)			66			
Yellow Warbler	(S)			22	22		
Audubon's Warbler	(O)	11					
Black-throated Gray Warbler	(S)			22	22		22
Townsend's Warbler	(S)		22	22	22		
MacGillivray's Warbler	(S)			44	44		
Wilson's Warbler	(S)			44			
Brown-headed Cowbird	(S)			11	22		
Western Tanager	(S)			44	66		
House Finch	(S)			44	44		
American Goldfinch	(S)				66		
Rufous-sided Towhee	(P)	55	44	88	88	44	44
Oregon Junco	(P)	88	44	66	66	33	33
Chipping Sparrow	(S)			44	44		
Golden-crowned Sparrow	(O)			66			
Total species		23	21	30	30	14	16

¹ Converted to birds per 100 acres.

²P=permanent resident.

S=summer resident.

W=winter resident.

O=occasional resident.

occupancy). Summer residents included species which arrived in early or late spring, nested, and then left during the spring or summer periods. Occasional visitors were birds that moved through the area, foraged for a short period of time, and then left. This category included birds that visited the area during migration.

During the winter, most of the bird species formed flocks. Single-species flocks of Oregon Juncos (*Junco oreganus*), Ruby-crowned (*Regulus calendula*) or Golden-crowned Kinglets (*Regulus satrapa*), or Common Bushtits (*Psaltiriparus minimus*) were common. Mixed-species flocks generally included chickadees, nuthatches, creepers, and woodpeckers. The above flocks were the most common groupings of birds observed during winter. Birds found in the oaks during the winter consisted of permanent residents and a few winter residents such as Winter Wrens (*Troglodytes troglodytes*) and Varied Thrushes (*Ixoreus naevius*). Permanent residents of the higher-elevation coniferous stands which expanded their habitat occupancy became winter residents in oak stands. The fir and hemlock areas had no winter residents as such. All bird species recorded in these areas during the winter were permanent residents.

TABLE 4. Population census results for avifauna of Douglas-fir.

Species	(Resident Type) ¹	Winter	Early Spring	Season Late Spring	Early Summer	Late Summer	Fall
Turkey Vulture	(O)			11	11	5	
Red-tailed Hawk	(O)			1		1	
Blue Grouse	(P)		22				
Ruffed Grouse	(P)		22				
Great Horned Owl	(O)		1	1			
Rufous Hummingbird	(S)				22		
Hairy Woodpecker	(P)			22	22		
Downy Woodpecker	(P)			22			
Western Wood Pewee	(S)				44		
Steller's Jay	(P)			22	44	22	
Chestnut-backed Chickadee	(P)	176	198	154	66	176	132
Red-breasted Nuthatch	(P)	44	44	66	44	99	88
Brown Creeper	(P)	22	44	44	55	44	44
House Wren	(S)			22	44	44	
Winter Wren	(P)	22	22	44		22	22
Golden-crowned Kinglet	(P)	88			22		
Hutton's Vireo	(S)			22	22		
Solitary Vireo	(S)			22			
Orange-crowned Warbler	(S)			22			
Audubon's Warbler	(S)			22			
Townsend's Warbler	(S)			22			
Hermit Warbler	(S)			44	44	22	
MacGillivray's Warbler	(S)			22	22	22	
Wilson's Warbler	(S)			22	22		
Western Tanager	(S)			44	44		
Black-headed Grosbeak	(S)				22		
Purple Finch	(S)			22			
House Finch	(S)			11			
Pine Siskin	(S)		22				
Red Crossbill	(P)					44	
Rufous-sided Towhee	(P)			22			
Oregon Junco	(P)	22	22	66	44	66	110
Total species		6	9	24	17	12	5

¹P=permanent resident.

S=summer resident.

W=winter resident.

O=occasional resident.

Altitude as well as the presence or absence of foliage may play a role in the type of wintering species found in the areas. When the total number of individuals present during each of the seasons in the study areas was calculated as a percentage of the total for the season having the largest number of individuals, the values in oak stands were somewhat higher than those for coniferous areas (Table 6). An influx of winter residents was largely responsible for this difference. Only 69 percent of the individuals wintering in oaks were permanent residents, while 100 percent of the birds in conifers were permanent residents (Fig. 1).

During early spring, permanent residents in the study areas began to establish

TABLE 5. Population census results for avifauna of western hemlock.

Species	(Resident Type) ¹	Winter	Early Spring	Season Late Spring	Early Summer	Late Summer	Fall
Great Horned Owl	(O)			1			
Pileated Woodpecker	(O)		2	4			
Hairy Woodpecker	(P)			22	22	22	
Downy Woodpecker	(P)	22		22	22	22	
Hammond's Flycatcher	(S)			22	22	22	
Dusky Flycatcher	(S)			22	22	22	
Western Flycatcher	(S)			44	22	44	
Western Wood Pewee	(S)			22	22		
Gray Jay	(S)			22	22		
Chestnut-backed Chickadee	(P)	176	44	88	110	198	88
Red-breasted Nuthatch	(P)	66	22	44	22	44	22
Brown Creeper	(P)	44	22	22	22	44	22
Winter Wren	(P)	44	44	44	44	44	44
Varied Thrush	(O)	55					
Hermit Thrush	(S)			22			
Golden-crowned Kinglet	(P)			22	22	22	110
Hutton's Vireo	(S)				22		
Hermit Warbler	(S)			44			
MacGillivray's Warbler	(S)			22	22	22	
Wilson's Warbler	(S)		22	22			
Western Tanager	(S)			44	44		
Black-headed Grosbeak	(S)			22			
Evening Grosbeak	(S)			88			
Pine Siskin	(S)			22			
Red Crossbill	(P)	44	44	66			
Oregon Junco	(P)			44	44	44	88
Song Sparrow	(S)			22			
Total species		7	7	25	16	12	6

¹P=permanent resident.

S=summer resident.

W=winter resident.

O=occasional resident.

TABLE 6. Percentage of the maximum individual birds in each vegetation type.

Study Area	Winter	Early Spring	Season Late Spring	Early Summer	Late Summer	Fall
Oak	58.5	57.5	90.9	100.0 ¹	43.2	50.4
Fir	43.0	45.7	100.0	68.5	62.7	43.0
Hemlock	55.4	24.6	100.0	62.2	63.8	45.9

¹ The season with the highest total number of individuals was considered 100 percent in each study area.

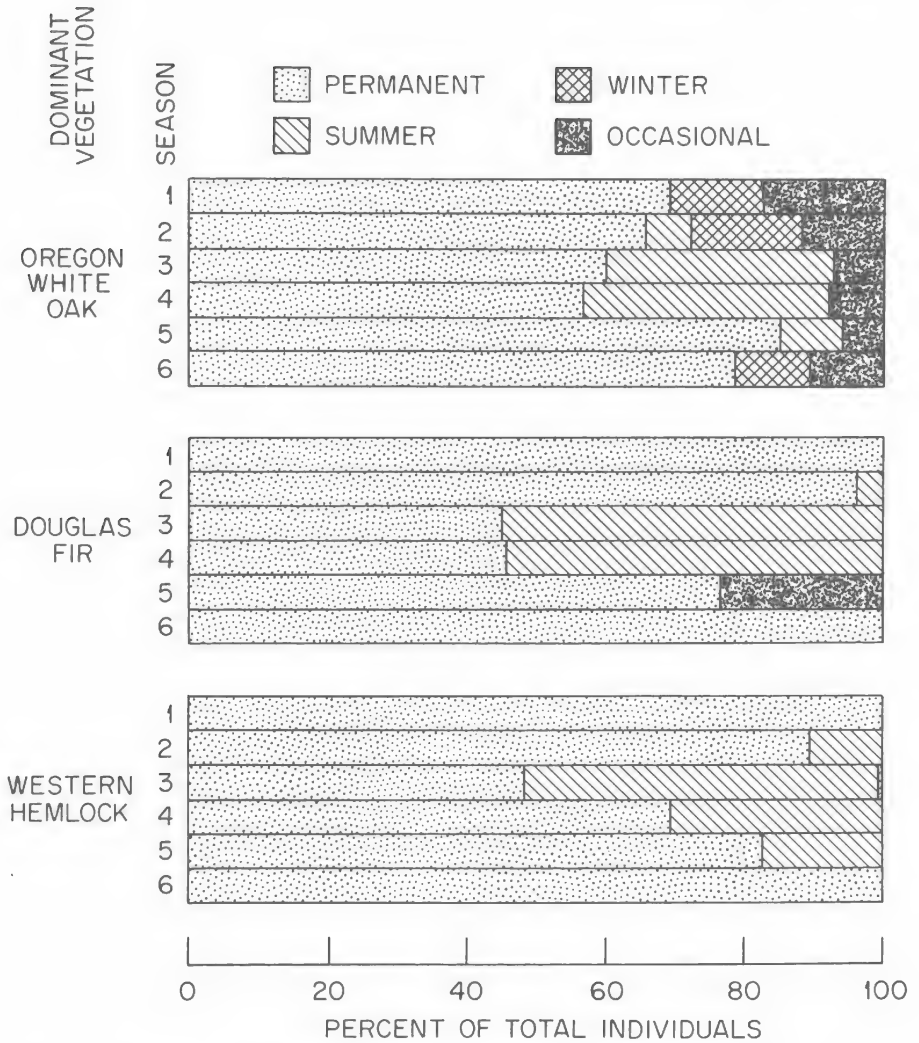


Figure 1. Comparison of residents in vegetation types. Season: 1=Winter, 2=Early Spring, 3=Late Spring, 4=Early Summer, 5=Late Summer, 6=Fall.

territories. Several summer-resident species arrived in all areas (Fig. 1); however, in most areas the total number of individuals decreased as bird species began to spread out (Table 6).

By the beginning of late spring, permanent-resident species were all nesting. During this period, a large influx of summer residents occurred (Fig. 1). There were no longer any winter residents in the oaks, as these species had withdrawn to their coniferous breeding habitats. Summer residents comprised 51 to 55 percent of all individuals

in the conifers while only 33 percent in the oaks. In the oaks, the summer residents were almost exclusively neotropical migrants (sensu MacArthur, 1959), which arrived, nested, and quickly departed. Some of the summer-resident species of the conifers were species which are characteristically nomadic in the forests and valleys of the Pacific Northwest during most of the year, but which select an area to nest during this period. Evening Grosbeaks (*Hesperiphona vespertina*) and Pine Siskins (*Spinus pinus*) were in this category. In most areas the late spring or early summer seasons had the highest total number of individuals for the year (Table 6), with little variation between the two seasons.

Most permanent residents had completed nesting by early summer and were dispersed throughout the area, no longer defending territories. The percent of all individuals which were summer residents remained high during this season (Fig. 1).

Summer residents generally completed nesting during late summer and left the forest. American Goldfinches (*Spinus tristis*) and Lazuli Buntings (*Passerina amoena*) nested in the oaks, while nests of Cedar Waxwings (*Bombycilla cedrorum*) were occasionally found in the conifers.

When compared to the spring and summer seasons, fall was a period of relative calm in the study areas. Most of the species were silent. Several species, including the chickadees, juncos, and bushtits, were found in small single-species flocks. In most areas the number of individuals was less than in the winter. Winter species occurred in oak stands while only permanent residents inhabited conifers (Fig. 1).

Diversity of Avifauna. To compare avian populations of the study areas during the different seasons, species diversity calculations were made. A number of indices of diversity have been proposed. Simpson (1949), Shannon and Weaver (1949), Margalef (1959), and McIntosh (1967) give examples of a few. In this study, I used the information theory diversity index (Shannon and Weaver, 1949).

The information theory species diversity index, H , is calculated:

$$H = -\sum_{i=1}^s p_i \log_e p_i,$$

where, s = the number of species,

p = the proportion of the total number of individuals which belong to the i^{th} species.

The values of this index can range from 0 ($\log_e$ of 1) if all of the individuals are of one species to $\log_e s$ if the number of individuals equals the number of species. The maximum diversity of a sample is thus given by:

$$H_{\text{MAX}} = \log_e s.$$

Comparison of the species diversity, H , of the avifauna in the three vegetation types is shown on a seasonal basis in Table 7. Total diversity was higher in the predominantly oak areas. For late spring, the breeding season for which most diversity indices in the literature have been calculated, the highest diversity (3.21) was obtained in the oaks. Diversity in Douglas-fir dropped to 2.97 and western hemlock rose to 3.07, showing a very close diversity in both conifers. When comparisons of H/H_{MAX} were made (Table 7), the late spring avifaunal diversity indices closely approached H_{MAX} ,

TABLE 7. Seasonal species diversity of avifauna in study areas.

Season	H	HMAX	H/HMAX
White Oak			
Winter	2.706	2.996	0.903
Early spring	2.826	3.045	0.928
Late spring	3.210	3.434	0.935
Early summer	3.234	3.434	0.942
Late summer	2.257	2.639	0.855
Fall	2.434	2.833	0.859
Douglas-Fir			
Winter	1.447	1.792	0.808
Early spring	1.718	2.197	0.782
Late spring	2.971	3.219	0.923
Early summer	2.825	2.890	0.977
Late summer	2.110	2.485	0.849
Fall	1.461	1.609	0.908
Western Hemlock			
Winter	1.701	1.946	0.874
Early spring	1.850	1.946	0.951
Late spring	3.070	3.219	0.954
Early summer	2.605	2.773	0.939
Late summer	2.151	2.485	0.865
Fall	1.673	1.792	0.934

indicating that individuals were fairly evenly divided among all species. In fact, during most of the year, the avifaunal diversity of the study areas was relatively close to HMAX. In the majority of comparisons H was at least 90 percent of HMAX.

Discussion

The gradient of vegetation analyzed for avifaunal composition in western Oregon includes three series of plant community succession (Franklin and Dyrness, 1969). Succession has been defined by Margalef (1969) as "... the occupancy of area by organisms involved in an incessant process of action and reaction which in time results in changes in both the environment and community." He further stated that during succession there was a trend toward increase in biomass, stratification, complexity, and diversity. Odum (1969) listed four types of diversity which could be observed during succession: species variety, expressed as a species number ratio; equitability, the apportionment of individuals among species; stratification; and biochemical diversity, the increase in diversity of organic compounds such as variety of plant pigments. Each of these components of diversity tended to go from low to high in the successional sequence and theoretically reached a stable state in the mature or climax stage. In this study, the measure of equitability species diversity was of primary concern.

If we assumed that species diversity of the avifauna followed the general trend of species diversity in succession, we should expect the bird species diversity of the study areas to increase in accordance with their successional status. Thus, the fir stands should have a higher diversity than the oak, and the hemlock a higher diversity than the fir. Rather, a definite drop in diversity occurred between the oak and fir while only a small rise was noted between the fir and hemlock.

Johnston and Odum (1956) studied the bird populations along a successional gradient in the Piedmont of Georgia and found a bimodal pattern of species abundance; the number of species increased during the early stages of old field succession, declined

during early forest stages, and then increased again in the mature forests. Odum (1969) suggested that during succession, an increase in potential niches resulted from increased biomass, stratification, and other consequences of biological organization exceeding the countereffect of increased size and competition of the organisms. While one would assume that diversity should increase for all species of organisms living in an area, this did not necessarily follow. Essentially the assumption was made that as communities became more complex, it became possible for animals to subdivide the area into finer and finer parts, thus reducing the size of niches. In terms of behavior, the animal had become more stereotyped (Klopfer, 1962). When the niche size was reduced, the range of objects in the environment to which the animal responded by feeding, reproducing, seeking shelter, etc. was reduced. As the oak-fir sequence did not follow the expected trend in diversity in relation to avifauna, several factors had to be considered. First, it was possible that a measure of diversity of all organisms of the communities, not just the birds, would have presented the expected increase in diversity with each step in succession. Also, it would have been important to measure the total biomass in the vegetative types to see if any change occurred there.

Second, in examining the three stages in succession, some marked differences in vegetation structure were apparent. The oaks had a much denser understory than undisturbed fir and hemlock communities. This might mean that a larger number of species could be accommodated in the more diverse vegetation.

Finally, the mobility of avian population should be considered when calculating diversity. Patchiness in the vegetation may in itself have accounted for part of the irregular distribution of the avian populations; however, each species of bird had a different ability to move through an area. This movement was influenced by features unique to each species.

When comparison was made with the bird species diversity values obtained in other studies, the results for this study were higher than those reported by MacArthur and MacArthur (1961) for eastern deciduous forests, and also exceeded those from Puerto Rico and all the mature and young tropical forests in Panama (MacArthur, Recher and Cody, 1966). Karr (1968) compared the species diversity in an east-central Illinois strip-mined area during the breeding season and found results in bottomland forests similar to this study. He suggested that the size of the area censused as well as the patchiness in vegetation and patchiness of bird distributions may have influenced the bird species diversity.

Total populations in the study areas in western Oregon were somewhat higher than the avian populations found in eastern forest communities. Johnston and Odum (1956) found 474 individual birds per 100 acres in southern pine and 448 birds per 100 acres in oak-hickory woods. Twomey (1945) reported 406 birds in an elm-maple forest during breeding season. Rohwer and Woolfenden (1969) found 308 birds in a mixed oak woods in Florida. Kendeigh (1944) found a range of 390 to 570 breeding birds per 100 acres in eight deciduous forests of the eastern United States. Bond (1957) recorded 310 to 386 individuals per 100 acres in the upland forests of southern Wisconsin. The range of 154 to 1112 in my study may have been partly the result of the large number of permanent residents in the Oregon forests. During the breeding season in Oregon, the numbers of individuals in the study areas ranged from 464 to 1112. The upper portion of this range exceeded the totals found in eastern forests.

MacArthur (1959) indicated that a very high percent (70-90) of eastern forest

species were migratory whereas only 20 to 30 percent of the Oregon forest species were neotropical migrants. My results indicated that 30-55 percent of the birds were summer residents. Oak stands had fewer summer residents (about 35 percent) while the fir and hemlock stands had 50-55 percent. Not all summer residents, however, were neotropical migrants. This was particularly true in the conifers where many nomadic birds settled to breed. In the oaks, the greater proportion of the summer residents were neotropical migrants, the Brown-headed Cowbird (*Molothrus ater*) being one exception. The fact that in the west a lower proportion of the breeding avifauna of an area migrates than in the east may have partially accounted for the relatively high numbers of birds found in the western Oregon forests when compared with eastern studies. The mild winters in the Willamette Valley undoubtedly allowed many bird species to find food during the winter period.

In western Oregon forests, with their rather stable environment and mild winters, a high proportion of the birds were permanent residents. Many of these permanent residents ranged over a wide area in the forests. The forests themselves were distinct, in that communities of upper-story vegetation were separated from each other by narrow ecotones, which contrasted to the many eastern forest communities which shared broad ecotones (Kendeigh, 1948). Much of the forest area in Oregon had been disturbed by man through logging and livestock grazing. Natural events such as windfall had disturbed other areas. Thus, there were "gap phases" within the forested areas. In this study, avian community structure did not conform to the plant community outline. There were some birds that might be classified with a deciduous or coniferous community (e.g., Black-capped Chickadee (*Parus atricapillus*) and White-breasted Nuthatch (*Sitta carolinensis*) in the former and Chestnut-backed Chickadee (*Parus rufescens*) and Red-breasted Nuthatch (*Sitta canadensis*) in the latter. Still, most birds did not confine themselves to either type of plant community, as was shown by juncos, creepers, and towhees. During the nonbreeding seasons, particularly, birds seemed less subjected to the confines of a particular plant community. All of the winter residents in the oaks were found as permanent residents in the conifers.

Summary

The avifaunal composition of 10 western Oregon forest stands located at the eastern base of the Coast Range was examined on a seasonal basis. The stands were dominated by Oregon white oak, Douglas-fir, and western hemlock. Avian populations were sampled monthly from January 1968 to January 1970, using permanent transects.

Oak-dominated stands had the highest bird species diversity in all seasons. This is in contrast to the expected increase in diversity with each successional sere. In most cases the actual species diversity was at least 90 percent of the maximum possible diversity.

All fir and hemlock stands shared a large number of species and supported roughly similar total populations. In the ecotonal areas, diversity was slightly higher than in the surrounding pure stands of either deciduous or coniferous vegetation.

More individuals and species were found in western Oregon forests than reported for forests in eastern United States. Further, a large proportion of the Oregon birds were permanent residents. The percentage of migratory birds was lower than in eastern forests because of this large number of permanent residents. These differences may in part stem from the milder winter climate characteristic of western Oregon.

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A Numerical Study of the Wing and Leg Muscles of Tinamou (Tinamidae)

Introduction

This paper is one of a series dealing with the gross anatomy of the wing and leg muscles of various families and orders of birds (Hudson and Lanzillotti, 1964; Hudson, Parker, Vanden Berge, and Lanzillotti, 1966; Hudson, Hoff, Vanden Berge, and Trivette, 1969).

Our aim is to determine to what extent the muscle patterns observed might contribute to an understanding of the systematic relationships of the various taxa.

This study gives a comparison of results obtained by treating the same set of data by two different methods of numerical analysis, one based on differential weighting of characters and expressed as cumulative scores of difference, and the other using correlation coefficients in which all characters are given equal weight.

The differential weighting of characters forming the basis for our cumulative scores is entirely arbitrary and subjective. This procedure assumes that all characters are not equally significant for taxonomic comparison, even though we have no objective way of making such distinctions and know nothing of the amount of genetic information involved in the production of these phenetic differences. In general we have given greater weight to the presence or absence of muscles and to muscle proportions of greatest relative magnitude.

Many of our measurements can be replicated by a careful operator, following our methods precisely (1964, p. 5), with deviations of $\pm .01-.02$ from the figures we have listed in Tables 1 and 2. In general the items most accurately measurable are those with a fixed point on a bone, such as the distal end of the Ent. ul. (Item 43) on the ulna and the proximal end of the Ul. meta. ven. (Item 52) on the ulna. Other items, involving an unfixed point such as the end of a muscle belly opposite a bone, for example, the distal end of the E. meta. rad. belly (Item 55), are subject to greater error—perhaps as much as .05 in some cases; however, the mean of several measurements should considerably reduce such error.

Measurements of the width of a muscle were made at a right angle to the di-

TABLE 1. Measurements and values used in quantitative comparisons of wing muscles.

	<i>Tinamus</i>	<i>Crypturellus</i>	<i>Nothoprocta</i>	<i>Nothura</i>	<i>Eudromia</i>	<i>Tinamotis</i>
Lat. dor. post. *160. Extent of origin from ribs and ilium	0	0	2.0	2.0	2.0	2.0
Cor. bra. post. 22. Ant. end of belly on Cor.	.41 (.36-.46)	.43 (.41-.45)	.32 (.29-.36)	.41 (.37-.44)	.40 (.39-.40)	.38
Subscp., P. int. 26. Post. end of muscle on Scap.	.42 (.41-.44)	.38 (.36-.39)	.33 (.28-.35)	.34 (.33-.35)	.36 (.35-.38)	.32 (.31-.32)
Subscp., P. ext. 27. Post. end of muscle on Scap.	.33 (.32-.34)	.38 (.34-.41)	.31 (.30-.32)	.34 (.31-.39)	.36 (.35-.36)	.41 (.41-.41)
Delt. maj. 31. Dist. end of belly opp. Hum.	.52 (.48-.59)	.61 (.60-.62)	.61 (.58-.63)	.60 (.58-.63)	.53 (.53-.53)	.38 (.37-.39)
Tri. scap. 149. Origin fleshy or tendinous	0 (Tendinous)	0.50 (Inter- mediate)	1.5 (←	1.5 Partly fleshy	1.5 →)	1.5
Pron. subl. 39. Dist. end of ins. on Rad.	.73 (.71-.74)	.82 (.78-.87)	.80 (.79-.80)	.85 (.79-.89)	.73 (.69-.75)	.61 (.60-.62)
Pron. prof. 41. Dist. end of ins. on Rad.	.50 (.46-.53)	.49 (.45-.53)	.53 (.52-.54)	.60 (.60-.61)	.61 (.57-.67)	.60 (.54-.65)
Ent. ul. 43. Dist. end of belly on ulna	.39 (.35-.43)	.44 (.42-.48)	.46 (.42-.49)	.52 (.51-.54)	.43 (.40-.45)	.40 (.39-.40)
F. dig. subl. 46. Prox. end of belly opp. ulna	.30 (.26-.34)	.38 (.35-.42)	.35 (.30-.41)	.31 (.25-.35)	.46 (.44-.47)	.44 (.43-.44)
Ul. meta. ven. 52. Prox. end of belly on ulna	.57 (.54-.60)	.59 (.56-.64)	.59 (.58-.60)	.53 (.51-.55)	.56 (.54-.57)	.68 (.68-.69)
E. meta. rad. 55. Dist. end of belly opp. Rad.	.73 (.70-.77)	.76 (.74-.79)	.81 (.80-.82)	.84 (.77-.87)	.76 (.75-.77)	.78 (.77-.80)
Supin. 57. Dist. end of belly on Rad.	.69 (.67-.70)	.67 (.66-.68)	.57 (.52-.60)	.52 (.50-.56)	.53 (.49-.57)	.40 (.40-.41)
Anc. 61. Dist. end of belly on ulna	.76 (.74-.77)	.85 (.79-.92)	.94 (.94-.94)	.95 (.92-.97)	.92 (.92-.93)	.75 (.74-.76)
E. ind. 1. 66. Distal head present or not	3.0 (Varies)	4.0 (Present)	4.0 (Present)	4.0 (Present)	0 (Absent)	0 (Absent)
Ul. meta. dor. 70. Dist. end of belly opp. Car. met.	.62 (.60-.64)	.62 (.58-.65)	.51 (.49-.54)	.53 (.49-.57)	.57 (.56-.58)	.52 (.51-.54)
158. Vent. belly present or not	4.0 (Present)	4.0 (Present)	4.0 (Present)	4.0 (Present)	4.0 (Present)	0 (Absent)
E. pol. br. 157. Dist. end of belly on pollex	.69 (.59-.78)	.72 (.69-.78)	.76 (.72-.79)	.69 (.46-.84)	.63 (.61-.66)	.75 (.68-.82)
Int. vol. 127. Dist. end of belly opp. Car. met.	1.0 (.97-1.04)	1.04 (.99-1.08)	.95 (.94-.97)	.92 (.88-.99)	.90 (.89-.92)	.92 (.90-.94)
F. dig. III 159. Dist. end of belly opp. Car. met.	.87 (.78-.93)	.78 (.76-.79)	.88 (.86-.90)	.83 (.81-.84)	.85 (.83-.87)	.86 (.85-.87)

*Item number

TABLE 2. Measurements and values used in quantitative comparisons of leg muscles.

	<i>Tinamus</i>	<i>Crypturellus</i>	<i>Nothoprocta</i>	<i>Nothura</i>	<i>Eudromia</i>	<i>Tinamotis</i>
II. troc. med.						
201. Separate or fused with II. troc. ant.	0 (Fused)	0 (Fused)	2.5 (Partly fused in some)	3.0 (Separate)	3.0 (Separate)	1.5 (Varies)
Fem. tib. ext.						
206. Prox. end of belly on Fem.	.40 (.38-.41)	.38 (.36-.41)	.34 (.30-.38)	.36 (.33-.41)	.27 (.25-.28)	.36 (.35-.36)
Fem. tib. int.						
318. Prox. end of belly on Fem.	.26 (.26-.28)	.21 (.19-.24)	.21 (.20-.23)	.21 (.20-.23)	.22 (.21-.24)	.29 (.29-.29)
Pirif., P. caud. fem.						
207. Present or absent	6.0 (←	6.0 (←	6.0 (←	6.0 (←	0 (Absent)	6.0 (Present)
209. Max. W. of belly ÷ L. of Fem.	.10 (.07-.11)	.11 (.07-.16)	.19 (.16-.21)	.21 (.16-.29)	0 *	.17 (.15-.19)
Pirif., P. il. fem.						
367. Extent of tendinous area	2.0 (Very large)	2.0 (Very large)	0 (←	0 (←	0 (←	0 (←
Pirif.						
295. Dist. edge of ins. on Fem.	.42 (.41-.42)	.39 (.37-.40)	.40 (.38-.41)	.43 (.41-.45)	.47 (.45-.48)	.42 (.42-.43)
Acc. Semit.						
214. Prox. end on Fem.	.67 (.62-.70)	.63 (.58-.66)	.46 (.42-.49)	.49 (.44-.57)	.58 (.58-.59)	.68 (.67-.68)
Isch. fem.						
218. Distance from post. end to Fem. ÷ L. of Fem.	.56 (.55-.58)	.50 (.45-.53)	.44 (.39-.49)	.47 (.43-.49)	.48 (.48-.49)	.46 (.42-.49)
Obt. int.						
299. Max. W. ÷ L. behind ant. edge of F. obt.	.48 (.45-.54)	.73 (.63-.81)	.69 (.65-.76)	.67 (.52-.88)	.65 (.59-.72)	.60 (.59-.60)
Add. long.						
301. Prox. end of ins. on Fem.	.61 (.55-.70)	.50 (.46-.54)	.47 (.45-.48)	.46 (.45-.47)	.54 (.52-.57)	.52 (.50-.55)
Tib. ant.						
327. Prox. edge of ins. on Tar. met.	.12 (.12-.13)	.12 (.11-.13)	.16 (.13-.17)	.16 (.16-.16)	.15 (.15-.16)	.18 (.18-.18)
Ext. dig. 1.						
368. One or two branches to Dig. II	0.5 (Two)	0.5 (Two)	0.5 (Two)	0.5 (Two)	0 (One)	0.5 (Two)
369. Insertion of medial branch to Dig. III on Phal. 2 (Phal. 2 only) only or ungual also	0 (No)	0.5 (Both)	0.5 (Both)	0.5 (Both)	0.5 (Both)	0 (Phal. 2 only)
370. Lateral branch to Dig. III fused with Ext. pro. d. III or not	0.5 (No)	0.25 (Partly)	0.25 (Partly)	0.25 (Partly)	0 (Fused)	0 (Fused)
371. Two or three branches to Dig. IV	0.5 (Three)	0.5 (Three)	0.5 (Three)	0.5 (Three)	0 (Two)	0.5 (Three)
Per. long.						
232. Belly ends opp. Tib. tar.	.82 (.80-.85)	.75 (.71-.77)	.74 (.72-.77)	.73 (.68-.78)	.74 (.73-.74)	.72 (.72-.72)
235. Sesamoid in dist. shank or not	0	.50	0	0	0	0

TABLE 2. (continued)

Per. brev.	6.0	6.0	6.0	6.0	6.0	0
302. Present or absent	(←	Present	→)	(←	Present	→)
Gas.						
241. Belly ends opp. Tib. tar.	.76 (.73-.79)	.67 (.65-.73)	.72 (.70-.75)	.73 (.70-.75)	.68 (.66-.70)	.74 (.71-.78)
303. Tendons of P. ext. and P. int. fuse opp. Tib. tar.	.80 (.77-.82)	.75 (.71-.78)	.75 (.74-.76)	.78 (.76-.79)	.74 (.71-.76)	.86 (.82-.90)
Plantaris						
246. Dist. end of belly opp. Tib. tar.	.41 (.38-.43)	.32 (.29-.35)	.37 (.35-.39)	.37 (.34-.42)	.38 (.34-.43)	.42
F. p. et p. d. II						
248. Belly ends opp. Tib. tar.	.38 (.35-.42)	.34 (.27-.42)	.47 (.42-.56)	.48 (.46-.50)	.38 (.34-.40)	.49 (.47-.51)
Flex per. d. II						
255. Belly ends opp. Tib. tar.	.72 (.68-.74)	.63 (.61-.65)	.65 (.62-.69)	.66 (.63-.69)	.67 (.62-.70)	.68 (.67-.69)
F. hal. 1.						
269. Dist. end of belly opp. Tib. tar.	.33 (.32-.36)	.34 (.33-.37)	.48 (.41-.56)	.53 (.52-.55)	.50 (.44-.56)	.44 (.42-.45)
343. Branch to hallux present or not	2.0 (←	Present	→)	2.0 (←	None	→)
336. Deep flexor tendons fused or connected by a vinculum	0 (←	Fused	→)	2.0 (←	Vinculum	→)
Ext. hal. 1.						
340. Prox. end of belly on Tar. met.	.44 (.33-.53)	.50 (.32-.60)	.19 (.18-.21)	.18 (.16-.20)	0 *	0 *
308. Present or absent	5.0 (←	Present	→)	5.0 (←	Absent	→)
Ext. pro. d. III						
365. Prox. end of belly opp. Tar. met.	.08 (.04-.11)	.06 (.04-.11)	.12 (.09-.15)	.07 (.05-.09)	.15 (.12-.20)	.14 (.12-.15)
372. Dist. end of belly opp. Tar. met.	.43 (.41-.44)	.50 (.46-.53)	.51 (.44-.57)	.46 (.33-.59)	.61 (.55-.69)	.57 (.54-.60)
F. hal. brev.						
363. Present or absent	5.0 (←	Present	→)	5.0 (←	Absent	→)
F. hal. brev.						
353. Prox. end of belly opp. Tar. met.	.47 (.43-.58)	.45 (.30-.56)	.13 (.07-.25)	.08 (.06-.09)	0 *	0 *
Add. d. II						
366. Present or absent	5.0 (←	Present	→)	5.0 (←	Absent	→)
Lumbricalis						
373. Lateral head from dist. end of F. hal. 1. tendon or not	0 (←	No	→)	1.5 (←	Yes	→)

*Not computed

rection of the fibers; in cases where the fibers are not all parallel this measurement was necessarily an approximation.

Very likely some error in measurements was due to different degrees of flexion of legs and wings before hardening in the preservative; however, we believe that this is a minor factor.

It is readily apparent that our mean values of muscle measurements are based on very small samples, in some cases on only one specimen. Obviously the study of additional material will change many of these values. In closely related birds, we believe that such changes would, for the most part, tend to bring the means closer together.

Bone measurements used in quantitative comparisons are the overall maximum taken in millimeters to the nearest 0.5 (to 0.1 in small specimens), with the Vernier caliper blades held at a right angle to the longitudinal axis of the bone. Muscle measurements were made in the same way. Measurements of muscles on or opposite skeletal parts were made from the extreme proximal end of the bone and are expressed as a percentage of the length of the bone used for comparison.

There is no special significance to our scoring myological differences on a scale of 0 to 6 points; this method simply seemed to us to be as good a scheme as any. Other scales, such as 0 to 10 or 0 to 100, would give very different figures, but these would show the same relationships between taxa if the same general philosophy of allotting values were followed. In scoring myological characters not involving measurements it was necessary to make, in each case, a subjective evaluation of the importance of the difference and to allot a score accordingly. In the numerous cases in which we compared the position of a muscle on or opposite a bone, we multiplied the difference times five because we felt that on a scale of 0 to 6 points this approach would yield a value commensurate with our idea of the importance of such a difference; e.g., a difference of 50 per cent of the length of the associated bone would give a score of 2.5 points.

The following illustrate the values we assigned to differences of various magnitude.

1. Presence or absence of a major muscle, e.g., the P. caud. fem. of the Pirif.—0-6 points.
2. Presence or absence of a small muscle, e.g., the distal head of the E. ind. 1.—0-4 points.
3. Differences in extent of origin, e.g., the Lat. dor. post.—0-2 points.
4. Maximum width of a muscle in relation to the length of an adjacent bone, e.g., the P. caud. fem. of the Pirif.—

$$\frac{\text{value}^1 - \text{value}^2}{\text{mean for all genera}} \times 2 = \text{score of difference.}$$

5. Position of the proximal or distal end of a muscle on or opposite an adjacent bone, e.g., the proximal end of the Ul. meta. ven.— $\text{Value}^1 - \text{Value}^2 \times 5 = \text{score.}$

Total scores of difference between pairs of genera for the legs and wings (Table 3) were derived by simply adding the scores for all 55 items. We consider these cumulative scores summations of most of the differences in the appendicular muscles of the

TABLE 3. Cumulative scores and coefficients for Appendicular Muscle items, comparing genera of Tinamou.

	<i>Crypturellus</i>	<i>Nothoprocta</i>	<i>Nothura</i>	<i>Eudromia</i>	<i>Tinamotis</i>	
<i>Tinamus</i>	5.25	10.25	10.75	11.55	17.65	Wing score
	.54	— .35	— .50	— .33	— .44	Wing Coef.
	6.76	19.91	20.21	31.58	33.17	Leg score
	.18	— .59	— .50	— .38	— .09	Leg Coef.
	12.01	30.16	30.96	43.13	50.82	Total score
	.27	— .49	— .49	— .38	— .20	Mean Coef.
<i>Crypturellus</i>		7.60	8.40	12.20	19.00	
		— .42	— .26	— .43	— .46	
		16.90	18.32	29.35	34.23	
		— .16	— .25	— .33	— .51	
		24.50	26.72	41.55	53.23	
		— .26	— .24	— .33	— .49	
<i>Nothoprocta</i>			3.40	8.70	14.80	
			.36	— .30	— .16	
			2.82	26.93	32.79	
			.83	— .18	— .32	
			6.22	35.63	47.59	
			.62	— .21	— .25	
<i>Nothura</i>				7.90	15.30	
				.05	— .38	
				26.86	33.58	
				— .23	— .30	
				34.76	48.88	
				— .12	— .34	
<i>Eudromia</i>					9.40	
					.15	
					24.41	
					.02	
					33.81	
					.05	

taxa being compared. We do not claim that our weightings are the best that might be devised, but they are one way in which such comparisons can be attempted. The size of such scores, of course, depends on the number of items included in the comparisons, as well as on the magnitude of the differences encountered.

Much has been written about the importance of selecting suitable characters for numerical treatment (Sokal and Sneath, 1963: 84; Boyce, in Heywood and McNeill, 1964: 50). However, there is no general agreement as to how this can be done other than by the subjective judgment of the investigator. We have followed more or less of a shotgun approach to the selection of characters, including practically all of the muscle modifications that could be measured or placed in definite categories for all genera. It is possible that some of the characters we have used are linked genetically; nevertheless, we have considered all items as unit characters, since this method seemed to be the most feasible way to compare these data numerically. Our treatment of data also makes no attempt to distinguish between homologous and pseudohomologous characters (Bock, 1963a). The Tinamidae are a morphologically very uniform group, showing no marked divergences in body proportions. This characteristic seems to us adequate justification for treating as separate unit characters the numerous muscle proportions shown by measurements in Tables 1 and 2.

The taxonomic validity of such quantitative scoring of myological differences depends on certain basic assumptions:

1. Birds with similar musculature are closely related, unless convergence is involved, the closeness of relationship being inversely proportional to the total differences. Conversely, birds with dissimilar musculature are more distantly related, the remoteness of the relationship being directly proportional to the total differences.

2. Convergence can result in similarity of a few to several or more muscles—but *not in the total musculature*; hence similarity due to convergence can be readily recognized if a very large number of muscles in diverse parts of the body are considered.

3. A quantitative study of the musculature is a valid approach to the study of phylogenetic relationships if the results, in general, confirm relationships established on the basis of other criteria.

As might be expected in a taxonomic study involving many characteristics, we were confronted with the problem of what to include and what to leave out. In general, the small unilateral aberrations infrequently encountered were ignored, although a few of the more important ones were briefly described; but no attempt was made to include these in the quantitative scoring. A great many measurements were made in addition to those given in Tables 1 and 2, but were not used in our comparisons, either because their accuracy was questionable, or because they were so uniform among the genera studied that they would contribute little or nothing to a scoring of differences. In questionable cases we made a final decision on the basis of the range of values; a difference of 10 per cent or more between the minimum and maximum values for all the genera being required for inclusion in our computations. Those with a range of less than 10 per cent were usually omitted.

When making comparisons with the aim of indicating degrees of relationship, we feel that the use of numerous measurable characters tends to lessen the biases, the subjectivity, the arbitrariness inherent in all taxonomic studies. We still must select the characters, determine the values to be assigned to each variable character, and make a judgment. Even so, a numerical analysis based on many items is superior to one based on only a few.

In this study the cumulative scores for myological characters sometimes differ rather markedly from the correlation coefficients. The major distinction between the two is that the correlation analysis regards all characters of equal value, giving the same weight to a muscle that lacks a certain head or slip as to another one that inserts a few millimeters closer to the proximal end of the bone. The genetic information involved in the two cases must vary considerably, and so must their taxonomic significance.

In computing numerical coefficients the product moment correlation was used as a measure of the taxonomic distance between members of each pair of taxa. The values for most characters were continuous and, since their magnitudes differed among characters, standardization was required. This was accomplished by expressing each value for a given character as a deviation from the mean divided by the standard deviation for that character (see, for example, Sokal, 1961). The resulting mean and variance of the values for each character were zero and one, respectively.

In computing the correlation coefficient between two taxa, if the value for a character for one taxon was missing, the comparison was deleted. This practice introduced a slight bias in the results in that the eliminated value or values contributed to the original standardization procedure for the character in question. Due to the

large number of characters involved and because the number of missing values was small, this deficiency was deemed insignificant (also see Sokal and Sneath, 1963).

We are continuing to base the names of wing muscles on the premise that the digits of the wing are I, II, and III to avoid confusion. We are aware that Montagna (1945), Holmgren (1955), and others consider these digits to represent II, III, and IV.

Literature Review

The tinamous, Family Tinamidae, range throughout South America to the Straits of Magellan and north through Central America to central Mexico. Confined to the neotropics, this group numbers 45 species (Hellmayr and Conover, 1942), or 51 species by Peters' (1931) count, 33 by Mayr and Amadon's (1951) estimate. The morphological similarities of many of the species call for a revision. Few studies exist on the morphology of tinamous at any level. Most of the early anatomical investigators sought to establish basic differences between the various groups of birds in order to establish criteria for defining the various taxa, and as an aid to classification. In many cases, certainly where tinamous were involved, a single or, at most, a few specimens were available for examination.

Parker's (1862, 1866a, 1866b) osteological studies led him to conclude that tinamous shared their affinities with the various ratite orders rather than with the galliforms.

In his monograph of the comparative morphology of the palaeognathae and the neognathae, Pycraft (1900) strongly emphasized osteology over other systems and, for many characters, noted the intermediate nature of tinamous between the ratites and the galliforms.

Low (1928, 1942) held a somewhat similar viewpoint. In a series of studies on the phylogeny of ratites, he concluded that the tinamous share many morphological features with the ratites; but since they also possess anatomical adaptations for flight, this finding indicated a later divergence of tinamous from the ancestral group that also gave rise to ratites. He maintained that tinamous bridged the gap between the cursorial and flightless ratites and the more "advanced" carinate birds.

Craigie's (1940a, 1940b) studies of the cerebral hemispheres supported the results of others who placed the tinamous and ratites together in the group Palaeognathae.

On the basis of his study of the bony palate, McDowell (1948) stated that the palate of tinamous "... is remarkably similar in basic pattern to that of the Rheidae, ..." although differing in detail, particularly in the proportions of the various elements of the palate.

Parkes and Clark (1966) added evidence from zoogeography and from structural characters of the rhamphotheca supporting the monophyletic origin of the tinamous and ratites "... from a family of 'prototinamous.'"

Some studies led to quite different conclusions, however. Thus, Chandler (1916) evaluated the phylogenetic arrangement of avian families and orders on the basis of feather structure, and placed the tinamous next to the Galliformes, stating that the former group "... should be considered as a specialized offshoot from a primitive gallinaceous stem."

Glenny (1946, 1955) noted the considerable likeness of the arterial arrangement-patterns of tinamous and gallinaceous birds, and the relatively greater dissimilarities of these patterns in tinamous and ratites.

Verheyen (1960a) employed primarily osteological characters in a study in which he concluded that tinamous belong within the order Galliformes. He also believed (Verheyen, 1960b) that outside the galliforms, the Rheas "... are the nearest relatives of the Neo-tropical tinamous."

Remarkably few systematic studies have been undertaken to establish relationships within the family Tinamidae. Salvadori's (1895) extensive catalogue of the specimens in the British Museum covered all the genera and species known at that time. Todd (1942) reviewed the systematics of the specimens in the Carnegie Museum. And Miranda-Ribeiro (1938) revised the tinamous found in Brazil.

Hellmayr and Conover (1942) undertook the most extensive review of tinamous to date. All of these works are largely, or entirely, based upon an examination of museum specimens. Von Boetticher (1934), on the other hand, went further, and considered habitat types as a taxonomic character. He confined his study almost entirely to the genera of tinamous.

Several revisions of tinamou genera have been undertaken. Brabourne and Chubb (1913, 1914) wrote short synopses of *Tinamus* and *Crypturellus*, and Conover (1950a, 1950b) made more extensive studies of *Eudromia* and *Nothura*. Again, criteria for their investigations were external characters.

The muscles of tinamous have received little attention except those considered taxonomically important. Thus, Alix (1874, 1876), Beddard (1898), Fürbringer (1902), Gadow and Selenka (1891), Garrod (1873, 1874, 1875), Lowe (1928, 1942), Mitchell (1913), and Pycraft (1900) describe certain muscles or muscle groups and make comparisons between various taxa. Alix (1874) made the most complete study of the muscles of any tinamous with an investigation of the myology of *Nothura major*. This study led him to view tinamous as closer to carinate birds in their relationships, while possessing a number of muscle and skeletal characters that resemble the ratites.

Myological studies generally confirm other anatomical evidence that shows a number of characters shared with both the ratites and the galliforms. Our study is apparently the only one in which myological characters have been used in comparing genera within the Tinamidae.

Materials

Specimens were preserved in 1:10 formalin solution and later transferred to 70 per cent ethyl alcohol. A few specimens were apparently preserved initially in alcohol. The numbers of appendages studied in detail are given below. Some of the qualitative variations were checked in all specimens available.

	Wings	Legs	Specimens
<i>Tinamus major</i>	5	4	3
<i>Crypturellus soui</i>	2	4	2
" <i>boucardi</i>	1	2	2
" <i>cinnamomeus</i>	1	0	1
" <i>tataupa</i>	0	0	2
<i>Nothoprocta ornata</i>	0	1	1
" <i>cinerascens</i>	1	2	2
" <i>pentlandii</i>	1	1	2
" <i>perdicaria</i>	1	0	1
<i>Nothura maculosa</i>	1	1	1
" <i>darwinii</i>	2	2	2
<i>Eudromia elegans</i>	2	2	2
<i>Tinamotis pentlandii</i>	1	2	1

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All of the myological data for this paper were studied in detail by Hudson and Schreiweis. Sy Ying Chen Wang made the initial dissections and measurements of most specimens. Lancaster collected the majority of the specimens studied, helped in writing the discussion and literature review, and furnished comments on taxonomic relationships based on non-myological data.

Abbreviations

Abbreviations of muscle names are given with the description of each; the following are in addition.

Ant., Anterior	Met., Metatarsale
Car.-met., Carpometacarpus	Obl. abd. ext., Obliquus abdominis externus
Coef., Coefficient	Obl. abd. int., Obliquus abdominis internus
Cor., Coracoid	Opp., Opposite
Cos. ster. ant., M. costisternalis anterior	P. ext., Pars externa
Cos. ster., costisternalis	P. int., Pars interna
Cris. lat. hum., Crista lateralis humeri	P. med., Pars media
Digit., Digit	P. ven., Pars ventralis
Dist., Distal	Phal., Phalanx
Fem., Femur	Post., Posterior
F. pneu., Foramen pneumaticum	Prox., Proximal
F. trios., Foramen triosseum	Rad., Radius
Hum., Humerus	Reg. intercon., Regio intercondyloidea
Ins., Insertion	Scap., Scapula
Int. cos. ext., Mm. intercostales externi	Ster. trach., M. sternotrachialis
Int. cos. int., Mm. intercostales interni	Tar.-met., Tarsometatarsus
L., Length	Tend., Tendon
Max., Maximum	Tib.-tar., Tibiotarsus
Mem. ster. cor. cl.,	Vent., Ventral
Membrana sterno-coraco-clavicularis	W., Width
Meta., Metacarpale	

Review of the Muscles of the Pectoral Limb

M. latissimus dorsi (Lat. dor.)

Latissimus dorsi anterior (Lat. dor. ant.)

The origin is by a narrow tendinous sheet from the mid-dorsal line (Fig. 1). Insertion is fleshy on the posterior surface of the humerus toward the ventral border as in *Gallus* (Fig. 2).

Latissimus dorsi posterior (Lat. dor. post.)

In *Tinamus* and *Crypturellus* the origin is very extensive, fleshy from the area between the origins of the Serr. sup. met. and Serr. sup. post., including parts of thoracic ribs 2, 3, and 4; partly fleshy from the lower part of the vertebral portion of rib 5; partly fleshy from the antero-ventral corner of the ilium; and by a narrow tendinous sheet from the mid-dorsal line (Fig. 1).

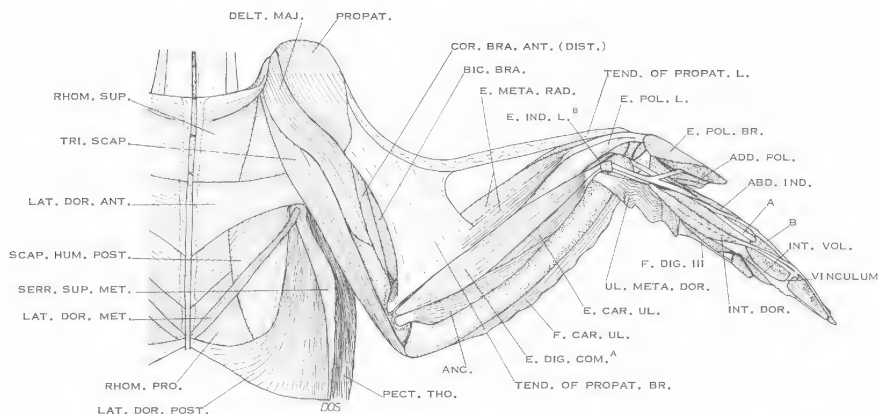


Figure 1. *Crypturellus tataupa*. Dorsal view of superficial muscles of the wing. Lat. dor. met. displaced anteriorly.

The origin in the other four genera is very different. There is no anterior extension between the Serr. sup. met. and Serr. sup. post. The origin is mainly tendinous from rib 5, partly fleshy from the upper portion of rib 4 and the entire anterior border of the ilium. The dorsal-most end of the origin is fleshy almost or quite to the mid-line. *Tinamotis* differs somewhat in having the origin more tendinous and the dorsal extension to the mid-line wider, resulting in a narrower gap between the Lat. dor. post. and Lat. dor. ant. Some *Nothoprocta* also have a narrow gap between these two parts of the Lat. dor.

The belly is narrowed anteriorly and inserts in the axillary region by a diffuse tendinous sheet which is attached to the skin, the Lat. dor. ant., the Delt. maj., and the Tri. scap. The Lat. dor. post. does not have a separate humeral attachment but is strongly connected to the tendinous band serving as the humeral origin of the Tri. scap.

Latissimus dorsi metapatagialis (Lat. dor. met.)

This weak, narrow ribbon of muscle arises from the mid-dorsal line and inserts on the Serr. sup. met., close to the point of attachment to the skin. In *Tinamus*, *Crypturellus*, and *Eudromia* the belly lies adjacent to the anterior border of the Lat. dor. post. In the other genera it passes over the dorsal surface of that muscle.

M. rhomboideus superficialis (Rhom. sup.)

Origin by a narrow, tendinous, sheet from the mid-dorsal line (Fig. 2). The insertion is fleshy on the medial and part of the dorsal surface of the scapula. The anterior slip inserts on the acromial process of the scapula and the scapular tuberosity of the clavicle.

M. rhomboideus profundus (Rhom. pro.)

The origin is fleshy from the mid-dorsal line (Fig. 3), except for a small tendinous area at the anterior end in most specimens. Insertion is fleshy on the medial border and much of the ventral surface of the scapula, especially posteriorly. The

fleshy insertion covers the entire ventral surface of the posterior part of the scapula in all except *Tinamotis*.

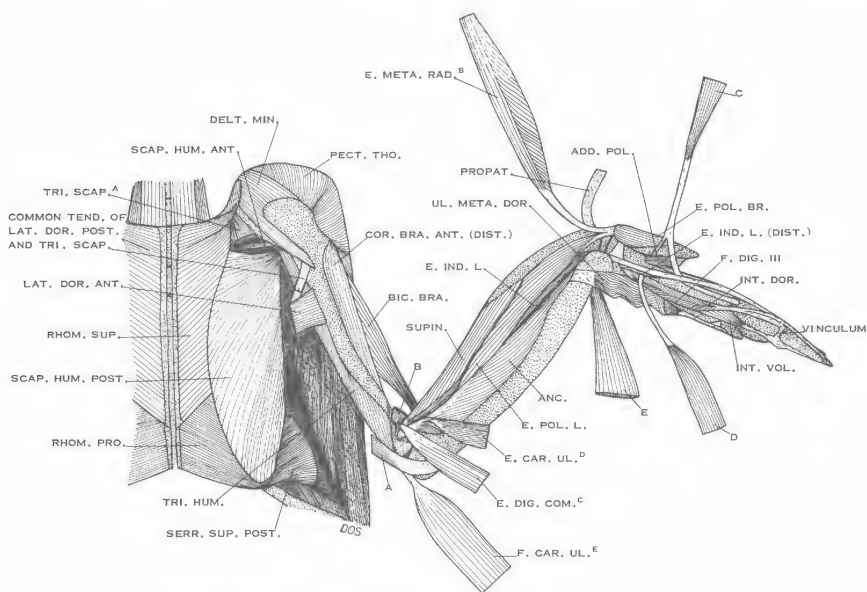


Figure 2. *Crypturellus tataupa*. Dorsal view of deeper muscles of the wing.

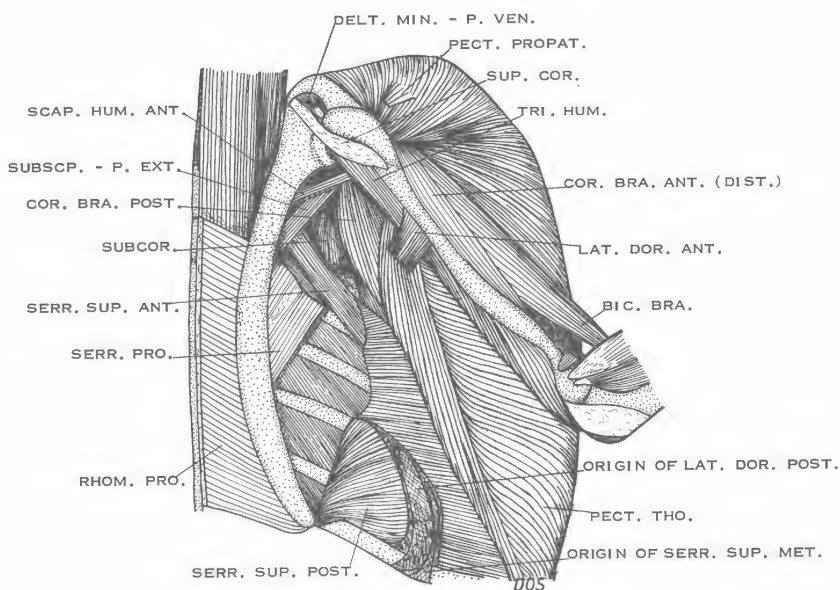


Figure 3. *Crypturellus tataupa*. Lateral view of some deep muscles of the thorax.

M. serratus profundus (Serr. pro.)

The Serr. pro. (Fig. 3) shows considerable variation in the number of fleshy slips. In some specimens there are three: a small anterior slip from the region of the transverse process of the third from last cervical vertebra, a larger slip mainly from the penultimate cervical rib, and another mainly from the last cervical rib. In some specimens only two slips were found. These fuse and have a single insertion on the medial surface of the scapula (Fig. 7).

M. serratus superficialis anterior (Serr. sup. ant.)

This muscle usually consists of a single head which arises fleshy from the ventral ends of the last two cervical ribs (Fig. 3). In *Crypturellus cinnamomeus* there are two slips proximally. In one *Nothoprocta* the origin extends to the first thoracic rib. The insertion on the scapula is between the heads of the Subscp. (Fig. 7) and is either tendinous or partly fleshy. In *Tinamus* the insertion is mainly posterior to the origin of the P. ext. subscp.

M. serratus superficialis posterior (Serr. sup. post.)

The Serr. sup. post. is a single sheet of muscle, usually without any definite digitations (Fig. 3), arising mainly fleshy from thoracic ribs 1, 2, 3, and 4, at the level of the uncinat processes. In a few specimens there is no attachment to rib 1 and (or) 4. In *Tinamus* and some *Crypturellus* (Fig. 7) the insertion on the scapula is all tendinous, but in most the posterior end is fleshy.

M. serratus superficialis metapatagialis (Serr. sup. met.)

The belly is long, narrow, and fleshy throughout (Figs. 1, 6) except for a partly tendinous attachment to rib 4 in some specimens. The origin is usually from ribs 3 and 4, just below the uncinat processes. In one *Nothura* the origin is on ribs 2, 3, 4; in another from rib 4 only. The insertion is on the medial side of the posterior end of the humeral feather tract as usual.

M. scapulohumeralis anterior (Scap. hum. ant.)

In tinamous the Scap. hum. ant. is very weak and slender (Fig. 3); fleshy throughout as usual. Weakest in *Tinamus*. The origin is from a small area on the latero-ventral edge of the scapula, just ventral and distal to the Tri. scap. Insertion is close to the distal or dorso-distal edge of the *For. pneu.* in most genera, but in *Eudromia*, one *Nothoprocta*, and *Tinamotis*, the insertion is more proximal, close to the insertion of the Cor. bra. post.

M. scapulohumeralis posterior (Scap. hum. post.)

The Scap. hum. post. arises fleshy from the most of the lateral surface of the scapula, beginning anteriorly at .22-.21 scapula, and extending to the posterior end (Fig. 2). Insertion is by a strong tendon on the proximal end of the bicipital crest of the humerus (Fig. 6). The insertion perforates the proximal end of the ventral head of the Tri. hum.

M. pectoralis

Pectoralis thoracica (Pect. tho.)

The powerful belly of the Pect. tho. arises fleshy from a very narrow line on the ventro-lateral edge of the sternal keel, from most of the long lateral ramus of the sternum, and the upper part of the adjacent sternal notch membrane, and from most of the ventral and lateral surfaces of the clavicle. The muscle is not divided into deep and superficial layers, but the dorso-lateral portion of the belly is fairly distinct (Fig. 3), with fibers directed more horizontally than in the rest of the muscle.

Insertion is mainly tendinous on the ventral surface of the *Cris. lat. hum.* The distal edge of the insertion is at .22-.33 hum.

Pectoralis propatagialis

The belly of the Pect. tho. gives off near its insertion a fairly large, fleshy, slip (Fig. 3) which inserts on the antero-ventral edge of the single propatagialis muscle. Ventral to this slip there is also a more or less definite tendinous sheet from the Pect. tho. belly to the prepatagium.

Pectoralis abdominalis (Pect. abd.)

From the ventral surface of the ventral feather tract there arises a wide fleshy sheet of dermal muscle, beginning near the mid-ventral line opposite the middle of the Pect. tho. belly. The fibers converge dorsally and insert in the axillary region, mainly on the ventral edge of the Lat. dor. post.

If this really represents the Pect. abd. it is very different from this muscle as we have observed it in other groups of birds. It is not divided into two parts, does not arise in the pelvic region, and the insertion is not on the Pect. tho. tendon or on the humerus.

M. supracoracoideus (Sup. cor.)

The powerful belly of the Sup. cor. arises fleshy from most of the surface of the keel and body of the sternum, from about the ventral half of the sternal notch membrane, from much of the ventro-lateral surface of the coracoid, and from part of the *Mem. ster. cor. cl.* The muscle is bipennate as usual and extends through the *F. trios.* The tendon passes over the posterior surface of the external tuberosity and inserts on the postero-dorsal surface of the proximal end of the humeral shaft (Fig. 3). The distal end of the insertion varies from .17-.26 humerus.

M. coracobrachialis anterior (Cor. bra. ant.)

The Cor. bra. ant. is enormously developed in tinamous (Figs. 2, 6). The origin is from the dorso-lateral apex of the coracoid by a sheath-like tendon which is fused to the tendon of origin of the Bic. bra. and encloses a bundle of muscle fibers as in most birds. This short portion inserts on the humerus just proximal to the insertion of the Pect. tho., and is more or less distinct in some specimens from the huge distal part which inserts over most of the anterior surface of the humeral shaft, extending distally to the *M. brachialis.*

M. coraco-brachialis posterior (Cor. bra. post.)

The origin is fleshy from a small area on the lateral surface of the Suf. cor., the antero-lateral spine of the sternum, and from a narrow area on the dorso-lateral surface of the proximal portion of the coracoid (Table 1a, Item 22). Insertion is by a strong tendon (Fig. 5) on the internal tuberosity of the humerus, just proximal to the *F. pneu.*

M. sternocoracoides (Ster. cor.)

The origin is mainly fleshy from most of the medial, anterior, and lateral surfaces of the antero-lateral sternal spine. The strong belly inserts fleshy on the dorsal and medial surfaces of an extensive area on the coracoid (Figs. 6, 7). The distal end of the muscle is at .44-69 coracoid.

M. subcoracoides (Subcor.)

The Subcor. is a very stout muscle located on the medial side of the coracoid (Fig. 7). It arises fleshy from the lateral surface of the manubrial spine of the sternum and from the dorso-medial surface of the *Mem. ster. cor. cl.* The belly lies against the coracoid but is not attached to it. The proximal end of the belly

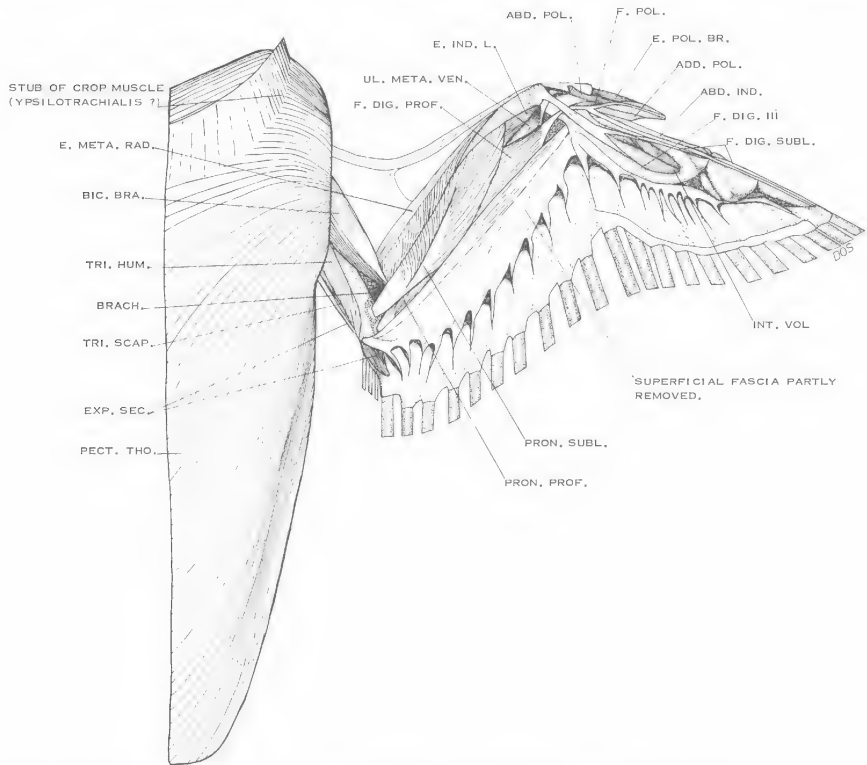


Figure 4. *Crypturellus tataupa*. Ventral view of superficial muscles of the wing.

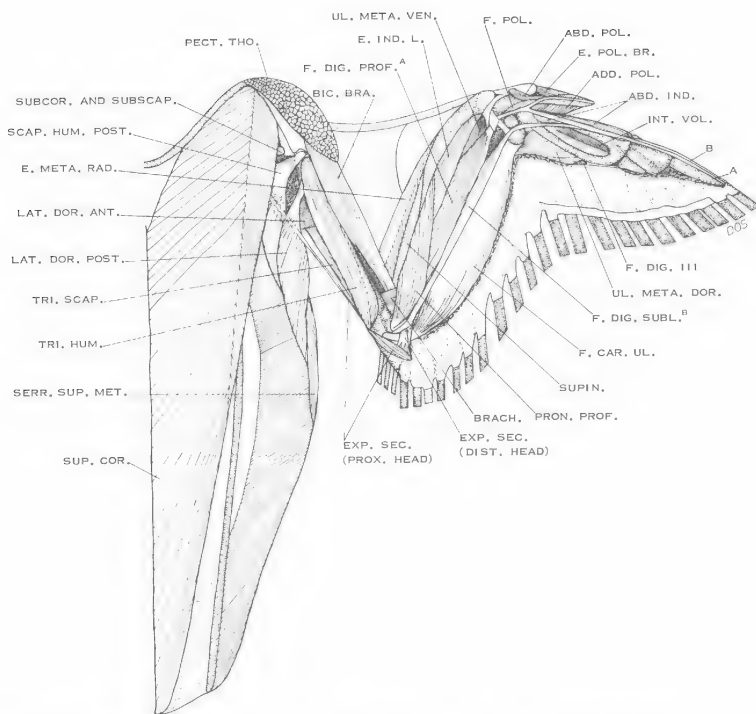


Figure 5. *Crypturellus tataupa*. Ventral view of deeper muscles of the wing.

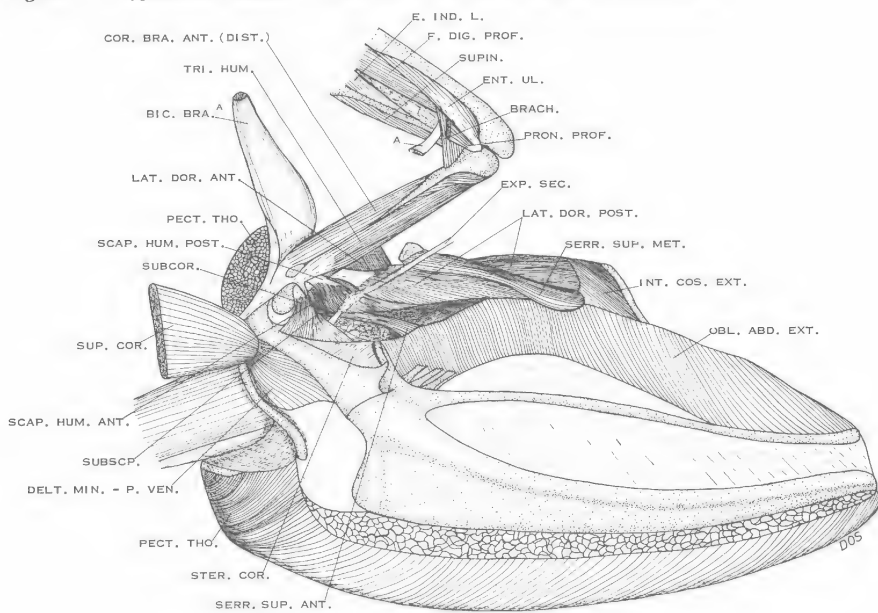


Figure 6. *Crypturellus tataupa*. Lateral view of deep muscles of the thorax.

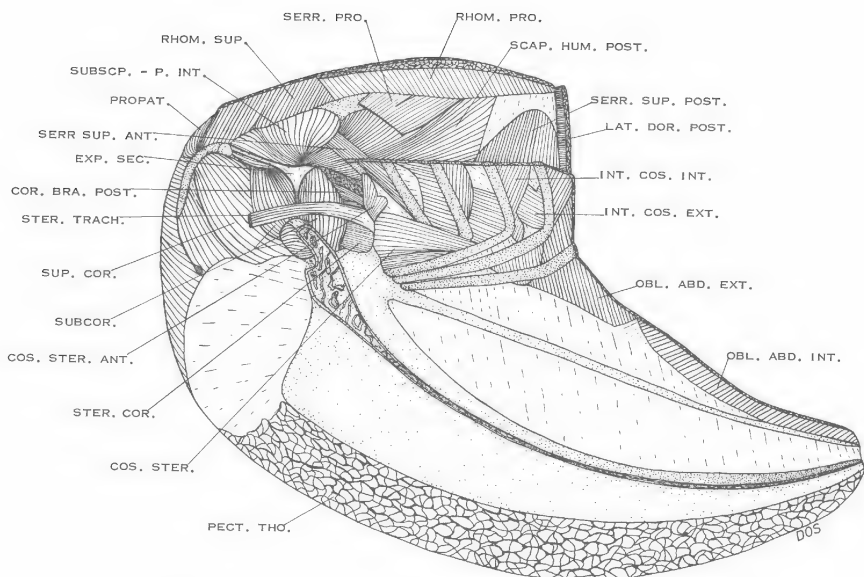


Figure 7. *Crypturellus boucardi*. Medial view of deep muscles of the thorax.

is located opposite .06-13 coracoid. The medial surface is more or less deeply grooved by the tendon of the Exp. sec. Insertion is by a very short tendon on the internal tuberosity of the humerus in common with the Subscap.

M. subscapularis (Subscp.)

The Subscp. is divided as usual into two heads but there is considerable variation in their relative lengths. In most genera the two parts are about equal in length, but in *Tinamus* the P. ext. is distinctly shorter than the P. int.; in *Tinamotis* the P. ext. is distinctly longer (Table 1a, Items 26, 27). The insertion is by a very short tendon on the internal tuberosity of the humerus in common with the Subcor.

M. propatagialis (Propat. l. and b.)

This muscle is represented by a single, broad, belly (Fig. 1) which arises partly fleshy from the dorsal apex of the clavicle. Distally the muscle gives off a tendon to the prepatagium, representing the *propatagialis longus*, and a very broad tendinous sheet representing the *propatagialis brevis*. The tendon of the Propat. l. is fibroelastic except near the wrist, where it becomes tendinous. Insertion is diffuse over the wrist area. The Propat. b. inserts on the E. meta. rad.

M. deltoideus major (Delt. maj.)

The origin is partly fleshy from a very small area on the dorsal apex of the clavicle, just posterior to the origin of the propatagialis. The muscle is shortest in *Tinamotis* (Table 1a, Item 31). There is little or no fleshy attachment on the humerus, but the insertion is mainly by a thin, tendinous, sheet along both the

anterior and posterior edges. Distally the muscle ends in a short tendon in most genera; longest in *Tinamotis*; lacking in *Nothura* and some *Nothoprocta*.

M. deltoideus minor (Delt. min.)

The origin of the dorsal head is mainly fleshy from the dorsal apex of the coracoid and a small area on the adjacent scapula. The wide belly extends over the dorsal surface of the shoulder joint (Fig. 2) and inserts on a narrow, curving, line on the dorsal surface of the humerus. Ventrally it is closely attached to the joint capsule and the dorsal surface of the tendon of the long head of the Delt. min.

The long head of this muscle is completely fused proximally with the belly of the Sup. cor., and only separates from that muscle in the triosseal canal. The tendon appears to be a part of the dorsal portion of the joint capsule, but continues along the dorso-anterior surface of the articular head of the humerus, and terminates just proximal to the insertion of the Pect. tho.

M. triceps brachii (Tri. bra.)

Scapular head (Tri. scap.)

The Tri. scap. arises by two short tendons from the scapula; the anterior tendon from a point just posterior to the glenoid fossa, the other from the shaft of the scapula, ventral to the anterior end of the Scap. hum. post. Associated with the anterior tendon of origin there is an extensive dorsal fleshy attachment to the scapula in *Eudromia*, *Nothura*, *Nothoprocta*, and *Tinamotis*. The origin is all tendinous in *Tinamus* and some *Crypturellus*, slightly fleshy in *C. tataupa* and most *boucardi*. The belly also has a tendinous attachment to the humerus in common with the Lat. dor. post. in all except one specimen of *Tinamus*. The muscle is fleshy almost to the elbow (Fig. 1). Insertion is by a single tendinous sheet in common with the Tri. hum. on the proximal end of the ulna.

Humeral head (Tri. hum.)

The origin is mainly fleshy from most of the posterior surface of the humerus, but is partly tendinous ventro-proximally. Distally the belly extends to the dorsal surface of the humerus. The muscle is slightly notched proximally by the insertion of the Scap. hum. post.; deeply notched proximally by the *F. pneu.* and insertion of the Scap. hum. ant. in most genera; slightly notched in *Eudromia* and least of all in *Tinamotis*. In no case does the Lat. dor. ant. infringe upon the Tri. hum.

The muscle is partly fleshy to the elbow joint (Fig. 6). Insertion is by a common tendon with the Tri. scap.

M. biceps brachii (Bic. bra.)

This powerful muscle arises by a single, broad, tendinous sheet, partly from the antero-lateral apex of the coracoid and partly from the bicipital crest of the humerus. The only indication of a division of the belly is a shallow longitudinal groove on the deep surface. The muscle is partly fleshy almost to the elbow joint (Fig. 2) and inserts by very short but strong tendons on both the radius and ulna. The biceps slip is absent.

M. expansor secundariorum (Exp. sec.)

The short, distal, head of this muscle is very weakly developed in tinamous. In most cases we found this represented by about three minute slips arising from a tendinous sheet attached to the internal epicondyle of the humerus and the joint capsule (Fig. 5). These insert on wing quills at the elbow and should not be confused with more distal fibro-elastic slips attached to secondary quills.

The proximal head is much larger and has a distinctly fleshy appearance. It is firmly attached to about three wing quills at the elbow. The tendon extends proximally along the posterior surface of the Tri. hum., closely attached to the skin. In the axillary region the tendon is strongly attached to the distal end of the belly of the Lat. dor. post. and to the ventral edge of the Scap. hum. post. (Fig. 6). On the dorsal surface of the Subcor. the tendon is attached to the postero-lateral edge of a tough, tendinous, triangle. The ventral edge of this triangle forms a distinct tendon which passes through a groove on the medial surface of the Subcor., and is attached to the antero-lateral edge of the manubrial spine of the sternum. The anterior edge of the triangle forms a distinct tendon which extends in a groove on the ventro-medial edge of the P. Int. of the Subscp. to an attachment on the postero-medial edge of the acromial process of the scapula (Fig. 7).

M. brachialis (Brach.)

This muscle is fleshy throughout and arises from the antero-distal end of the humeral shaft and inserts on the ventro-proximal end of the ulnar shaft, precisely as in *Gallus* (Fig. 6). The distal end of the insertion is at .24-.32 ulna.

M. pronator sublimis (Pron. subl.)

The Pron. subl. arises by a very short tendon from the proximal entepicondylar prominence of the humerus. This muscle is very long in tinamous (Fig. 4), with the insertion mainly fleshy on a long line along the ventral surface of the radius. The proximal end of the insertion is at .12-.24 Rad., the distal end (Table 1a, Item 39) is at .61 in *Tinamotis*, much farther distally in other genera, especially in *Nothura*. On the ventral surface of the belly there is a prominent longitudinal fold.

M. pronator profundus (Pron. prof.)

The Pron. prof. arises by a very short tendon from a more or less definite entepicondylar prominence on the humerus. The muscle is closely fused proximally with the Ent. ul. (Figs. 5, 6). In one wing of *Tinamus* and in some *Nothura* the tendon of origin is fused with that of the Pron. subl. Insertion is mainly fleshy on the ventral surface of the radius, adjacent to the posterior edge of the Pron. subl. The proximal end of the insertion on the radius ranges from .12-.19. The muscle is somewhat shorter in *Tinamus*, *Crypturellus*, and *Nothoprocta* than in the other genera (Table 1a, Item 41).

M. entepicondylo-ulnaris (Ent. ul.)

The Ent. ul. arises in common with the Pron. prof. by a short tendon from the distal end of the humerus (Figs. 5, 6). The insertion is fleshy on the ventral

surface of the ulnar shaft. The muscle is shortest in *Tinamus* and longest in *Nothura* (Table 1a, Item 43).

M. flexor carpi ulnaris (F. car. ul.)

This powerful muscle arises by a strong tendon from the apex of the entepicondyle of the humerus (Fig. 5) and passes through the ulnar pulley. The belly is flattish and has on the dorsal surface a rather definite groove about as in *Gallus*. The posterior border of the muscle is strongly attached to the bases of the secondary remiges. On the ventral surface there is a heavy superficial fascia that binds the F. car. ul. to the F. dig. subl. Insertion is mainly tendinous on the proximal end of the ulnare.

M. flexor digitorum sublimis (F. dig. subl.)

The belly of the F. dig. subl. arises from the dorsal surface of the superficial fascia mentioned above. A thickened portion of this fascia is attached to the humerus between the tendon of the F. car. ul. and the Pron. prof. + Ent. ul., and functions as a tendon of origin of the F. dig. subl. The belly is longest in *Tinamus* and *Nothura*, shortest in *Eudromia* and *Tinamotis* (Table 1a, Item 46).

The tendon of insertion passes through a groove on the ventral surface of the ulnare and joins the tendon of the F. dig. prof. about midway the Car. met. (Fig. 5). Near the base of Phal. 1, Dig. II (III) the tendon ensheathes that of the F. dig. prof. Insertion is on the base of Phal. 2 and distally almost to the end of that bone. It is strongly attached to the tendon of the E. ind. I. at the base of Phal. 1 and the base of Phal. 2.

M. flexor digitorum profundus (F. dig. prof.)

The origin is fleshy from about the proximal two-thirds of the antero-ventral surface of the ulna. Proximally the belly lies anterior to the brachialis and is fused to the E. pol. I. The belly begins at .11-.19 ulna; ends at .86-.94. The tendon passes through a groove on the anterior surface of the pisiform process of the Car. met. Near the base of the pollex the tendon gives off a strong branch which inserts on much of the ventral surface of that bone (Fig. 5).

Beyond the middle of the Car. met. the main tendon lies close beside the tendon of the F. dig. subl. Opposite the base of Phal. 1, Dig. II (III) the tendon of the F. dig. subl. forms a more or less definite sheath about the F. dig. prof. Insertion is on most of the ventral surface of Phal. 2.

M. ulnometacarpalis ventralis (Ul. meta. ven.)

The origin is fleshy from the ventral surface of the distal portion of the ulna, distal and partly posterior to the origin of the F. dig. prof. The belly is distinctly shorter in *Tinamotis* than in other genera (Table 1a, Item 52). The insertion is typical on the antero-dorsal surface of the proximal end of the Car. met.

M. extensor metacarpi radialis (E. meta. rad.)

The origin of the E. meta. rad. is mainly tendinous from the antero-dorsal surface of the humerus, at the proximal end of the ectepicondylar prominence. The muscle is single, but on the dorsal surface a seam suggesting a partial division can be readily opened. Our measurements show the belly to be shortest in

Tinamus, longest in *Nothura* (Table 1a, Item 55). The tendon fuses with that of the E. pol. I. just before inserting on the antero-proximal end of Meta. I (II).

M. supinator (Supin.)

The origin is by a short tendon from the lateral epicondyle of the humerus, just distal to the origin of the E. dig. com. Insertion is fleshy on the anterior and dorsal surfaces of the proximal portion of the radius (Fig. 2). The muscle is very short in *Tinamotis*, much longer in *Tinamus* and *Crypturellus* (Table 1b, Item 57).

M. extensor digitorum communis (E. dig. com.)

The E. dig. com. arises by a short tendon from the lateral epicondyle of the humerus, just proximal to the origin of the supinator. The belly extends along most of the length of the forearm (Fig. 1) and ends at .77-.89 ulna. Near the end of the ulna the tendon passes through a loop of fibro-cartilage in company with the tendon of the E. car. ul. Beyond this loop the tendon gives off a stout branch that inserts on the postero-dorsal side of the pollex, a little distal to the base (Fig. 2). The main tendon continues distally in a shallow groove on the antero-dorsal surface of the Car. met. to the insertion on the base of Phal. 1, Dig. II (III).

M. extensor carpi ulnaris (E. car. ul.)

The origin is by a common tendon with the Anc., from the postero-distal surface of the dorsal side of the humerus (Figs. 1, 2). Proximally the belly is firmly fused with the Anc. The belly ends at .81-.91 ulna. The tendon inserts on the postero-dorsal edge of the Car. met. at .25-.33.

M. anconaeus (Anc.)

The origin is in common with the E. car. ul. as indicated above. The insertion is fleshy on much of the anterior and dorsal surfaces of the ulna. The muscle is shortest in *Tinamus* and *Tinamotis*, longest in *Eudromia*, *Nothura*, and *Nothoprocta* (Table 1b, Item 61).

M. extensor pollicis longus (E. pol. l.)

The E. pol. l. arises fleshy by two well-developed heads, one from a small area on the anterior surface of the ulna near the Bic. bra. insertion, the other from most of the length of the radius on the dorsal and posterior surfaces. The two heads fuse at about .30-.50 radius. The proximal end of the anterior head is at .08-.21 radius; the distal end of the belly at .91-1.01 radius. The short, stout, tendon fuses with the tendon of the E. meta. rad. at the wrist (Fig. 2).

M. extensor indicis longus (E. ind. l.)

The E. ind. l. arises fleshy from a long line on the posterior surface of the radius. Proximally the muscle is tendinous. The proximal end of the belly is at .35-.51 radius, the distal end near the wrist. The tendon curls over the antero-dorsal edge of the distal end of the ulna and inserts on the base of Phal. 1, Dig. II (III). It also has a strong attachment to the base of the proximal phalanx. The distal head of the E. ind. l. (Fig. 2) is present in all genera except *Eudromia* and *Tinamotis*.

In every case the insertion is fleshy on the main tendon. It is absent in one specimen of *Tinamus*.

M. ulnometacarpalis dorsalis (Ul. meta. dor.)

The origin is by a strong tendon from the distal end of the ulna, on the antero-dorsal edge (Fig. 2). The ventral head is very large in *Tinamus* and *Crypturellus*; smaller in *Nothoprocta*, *Nothura*, and *Eudromia*. In these genera it wraps around the posterior and dorsal surfaces of the smaller dorsal head and around the proximal portion of the F. dig. III. The ventral head inserts mainly on a tendinous sheet that covers the ventral surface of the F. dig. III. At the distal end it usually has a weak, tendinous, insertion on the ventral surface of the third primary. The ventral head is absent in *Tinamotis*.

The dorsal head is present and quite uniform in structure in all specimens. The insertion is fleshy on a small area on the dorsal surface of Meta. III (IV), about opposite the base of the second primary.

M. abductor pollicis (Abd. pol.)

The origin is entirely fleshy from the ventral surface of the distal end of the tendon of the E. meta. rad. (Fig. 5). Insertion is on the antero-ventral edge of Phal. 1, Dig. I (II), a little beyond the base. The muscle is partly fleshy to the insertion or nearly so in *Tinamus*, *Crypturellus tataupa*, *Eudromia formosa*, *Nothura*, and one wing of *Nothoprocta* and *Tinamotis*. The tendon is longest in other species of *Crypturellus* and some *Nothoprocta*.

M. flexor pollicis (F. pol.)

The origin is mainly fleshy from the ventral surface of the base of the Car. met., between the ankylosed Meta. I (II) and the pisiform process. The belly is very small and lies between the Abd. pol. and the tendon of the F. dig. prof. (Fig. 5). The insertion is mainly fleshy on the postero-ventral edge of Phal. 1, Dig. I (II), somewhat beyond the base. The entire muscle is absent in both wings of one *Tinamus*.

M. adductor pollicis (Add. pol.)

The Add. pol. arises fleshy from the antero-ventral border of Meta. II (III) opposite the pollex. The insertion is mainly fleshy on most of the posterior surface of Phal. 1, Dig. I (II) (Fig. 5) and on the bases of two alular quills. The distal end of the fleshy insertion ranges from .70-.88 pollex.

M. extensor pollicis brevis (E. pol. br.)

*Tinamou*s are peculiar in having the E. pol. br. arising from the common tendon of the E. meta. rad. and E. pol. l., with little or no attachment to the Car. met. (Fig. 1). In most *Crypturellus* there is a weak tendinous connection with the Car. met. and the insertion of the Ul. meta. ven., in addition to the main fleshy origin from the common tendon indicated above. The insertion is fleshy along most of the anterior surface of Phal. 1, Dig. I (II), but the extent varies considerably (Table 1b, Item 157). In nearly all specimens the E. pol. br. shows a more or less definite division into a deep and a superficial layer.

M. abductor indicis (Abd. ind.)

The origin of the Abd. ind. is fleshy from an extensive area on the antero-ventral and anterior surfaces of Meta. II (III), beginning proximally at the pisi-form process and extending almost to the distal end (Fig. 5). The belly is grooved near the proximal end on the ventral side for the tendon of the F. dig. prof. The short, stout, tendon runs distally to the insertion on the antero-proximal edge of Phal. 1, Dig. II (III), without any deviation.

M. interosseus dorsalis (Int. dor.)

The origin is fleshy from the middle of the dorso-proximal surface of the Car. met., from the dorso-posterior edge of Meta. II (III), and from the dorso-anterior edge of Meta. III (IV). The proximal end of the belly is perforated by the tendon of insertion of the E. car. ul. in *Tinamus*, in three wings of *Crypturellus*, in *Eudromia formosa*, in *Nothura darwinii* and in *Tinamotis*. In *Tinamus*, one wing of *Crypturellus boucardi*, and in *Tinamotis*, fleshy fibers of the Int. dor. arise from this tendon. The distal end of the origin from Meta. III (IV) ranges from .64-.77 Car. met., and the distal end of the belly is at .77-.87 Car. met. The muscle is bipennate and fills most of the interosseal space (Fig. 2).

Opposite Phal. 1 (Dig. II [III]) the tendon is divided into an anterior branch that inserts on the antero-dorsal edge of Phal. 2 to the base of Phal. 3, and a stouter, posterior, branch that inserts on the base of Phal. 2. The anterior branch is closely attached to the tendon of the E. ind. 1. and to the posterior branch of the Int. dor. at the base of Phal. 2. At this point there is a definite vinculum connecting the posterior tendon with the tendon of the Int. vol. (Fig. 2).

M. interosseus volaris (Int. vol.)

The Int. vol. arises fleshy from the posterior surface of Meta. II (III) and the anterior surface of Meta. III (IV). The bipennate muscle fills the interosseal space on the ventral side (Fig. 4). The belly extends beyond the distal end of the Car. met. in some wings of *Tinamus* and *Crypturellus* (Table 1b, Item 127). Distally the tendon passes over the posterior edge of Phal. 1 and ends near the distal end of Phal. 2 (Fig. 2). Along the posterior edge of the tendon there is a strong attachment to several primary quill follicles. Insertion is mainly on Phal. 2, Dig. II (III).

M. flexor digiti III (F. dig. III)

The origin is fleshy from much of the posterior surface of Meta. III (IV) and part of the dorsal surface. Proximally the muscle is narrow and tendinous, beginning at .21-.34 Car. met.; very stout midway. Most of the F. dig. III is ensheathed proximally by the ventral head of the Ul. meta. dor. (Fig. 2). The belly extends farthest distally in *Tinamus* and *Nothoprocta* (Table 1b, Item 159). The rather long tendon inserts on a small tubercle on the posterior side of Dig. III (IV), as usual.

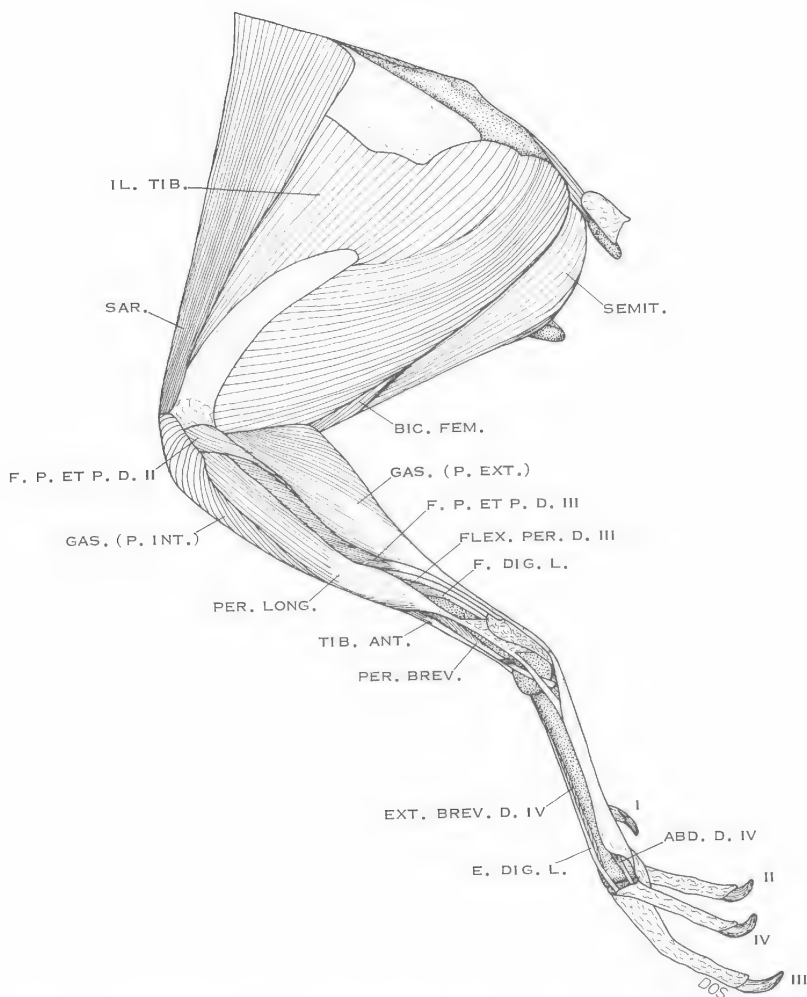


Figure 8. *Crypturellus tataupa*. Lateral view of superficial muscles of the leg. Posterior part of abdomen and most of tail muscles are not shown.

Review of the Muscles of the Pelvic Limb

M. iliotrochantericus posterior (Il. troc. post.)

The origin is fleshy from most of the preacetabular ilium, the belly broad and stout; divided anteriorly into a superficial muscle layer which is attached to a superficial tendinous sheet, and a deeper layer arising directly from the ilium. Insertion is by a wide tendon on the lateral side of the trochanter (Fig. 10).

M. iliotrochantericus anterior (Il. troc. ant.)

Arises fleshy from most of the ventro-lateral edge of the preacetabular ilium,

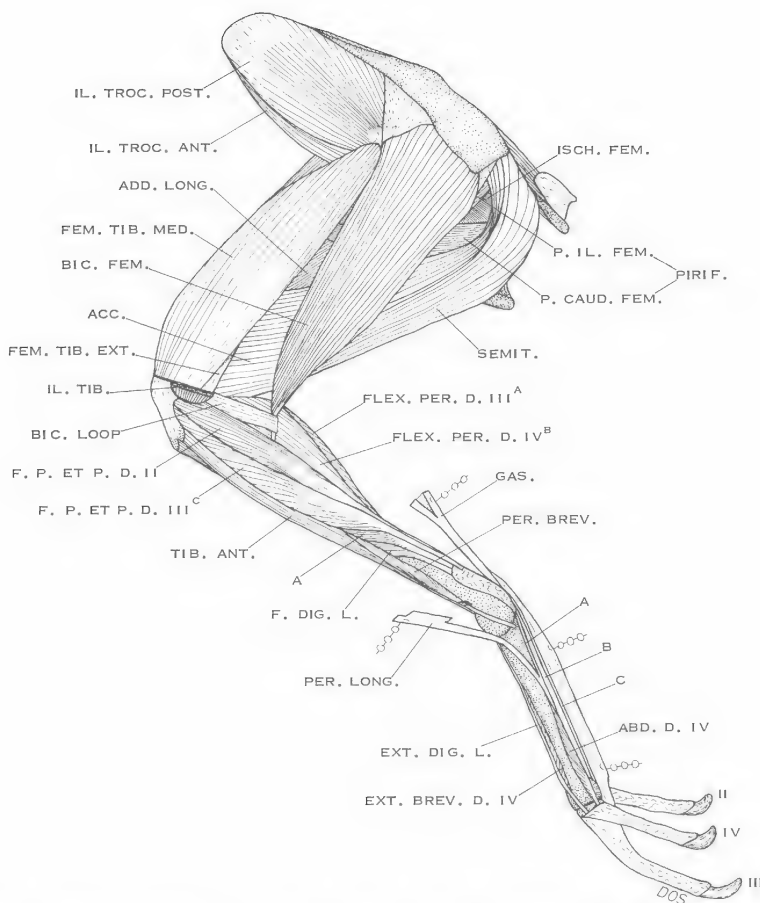


Figure 9. *Crypturellus tataupa*. Lateral view of a deeper layer of muscles of the leg.

strongly attached to the Il. troc. post. In *Tinamus* and *Crypturellus* this muscle is completely fused with the Il. troc. med. (Fig. 11); the two are quite distinct in *Eudromia*, *Nothura*, *Nothoprocta* and one leg of *Tinamotis*. The tendon of insertion is covered laterally by the tendon of the Il. troc. post. and the proximal end of the belly of the Fem. tib. med.

M. ilirotrochantericus medius (Il. troc. med.)

Fused throughout with the Il. troc. ant. in *Tinamus* and *Crypturellus*. Separate in *Eudromia*, *Nothura*, *Nothoprocta*, and one leg of *Tinamotis*, the origin from the ventro-lateral edge of the preacetabular ilium posterior to the Il. troc. ant. The area of insertion of the short tendon is rather widely separated from that of the Il. troc. ant. in *Eudromia* and one leg of *Tinamotis*; the insertions adjacent in *Nothura* and some *Nothoprocta*, the two fused in some of the latter.

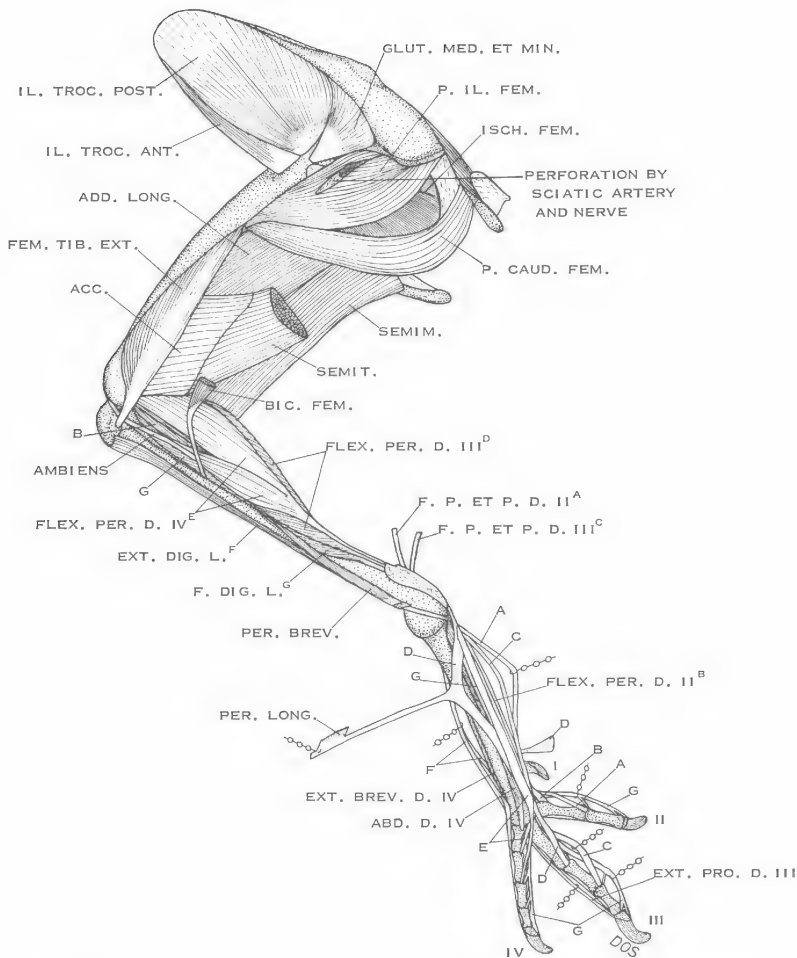


Figure 10. *Crypturellus tataupa*. Lateral view of a deeper layer of muscles of the leg.

M. gluteus medius et minimus (Glut. med. et min.)

Similar in all, the origin fleshy from the anterior iliac crest dorsal and posterior to the acetabulum (Fig. 11). The flat, triangular belly is well developed. The tendon crosses over the lateral surface of the tendon of the Isch. fem. except in some *Crypturellus*, and inserts just anterior to that muscle. The distal end of the tendon is covered by the proximal end of the Fem. tib. med. and that muscle has fleshy fibers arising from the tendon of the Glut. med. et min.

M. iliacus (Iliacus)

Similar in all, the origin fleshy from a small area on the ventral border of the ilium just medial to the posterior end of the origin of the Il. troc. ant. and med.

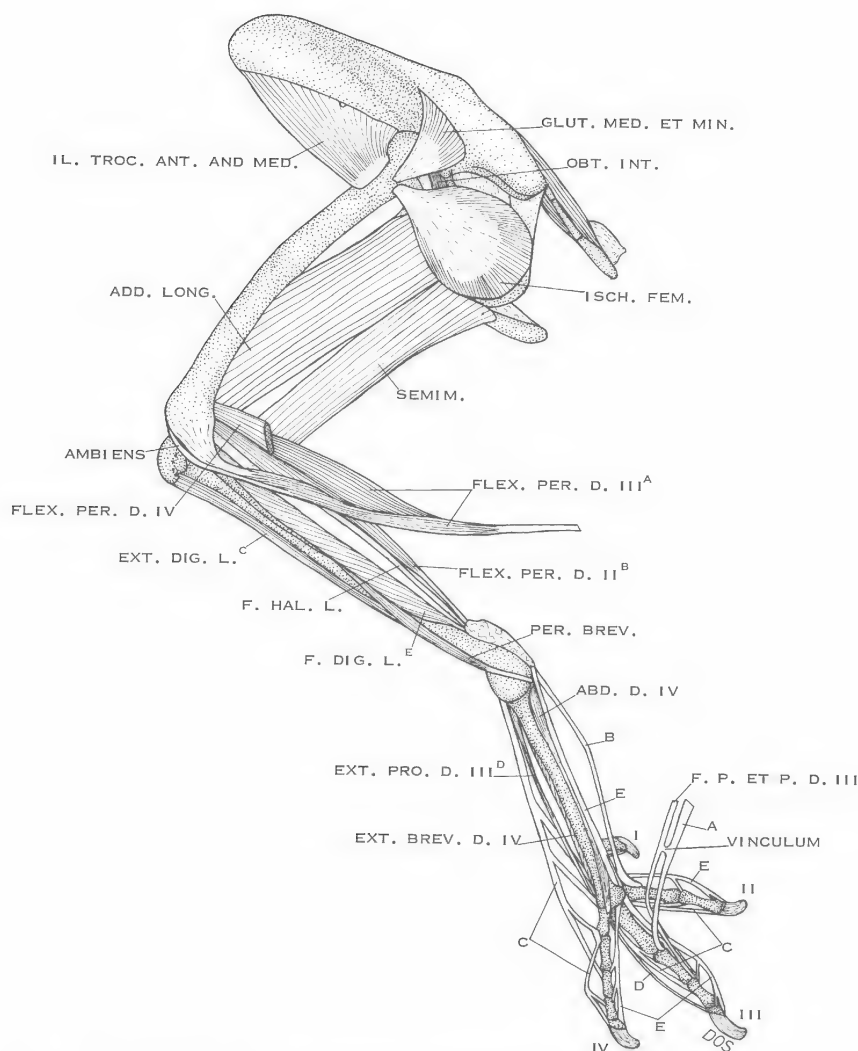


Figure 11. *Crypturellus tatanpa*. Lateral view of deepest muscles of the leg.

The muscle is much weaker than in *Gallus*, is fleshy throughout and distinctly widened at the insertion (Fig. 13).

M. ambiens (*Ambiens*)

The origin from the pectineal process of the ilium is by a short tendon in *Tinamus* (Fig. 13), partly fleshy in all others. The strongly developed belly shows considerable individual variation in relative length, but little difference between genera. The tendon passes around the lateral side of the knee, embedded in the patellar tendon as usual, and inserts on the tendinous origin of the lateral head of the flexor per-

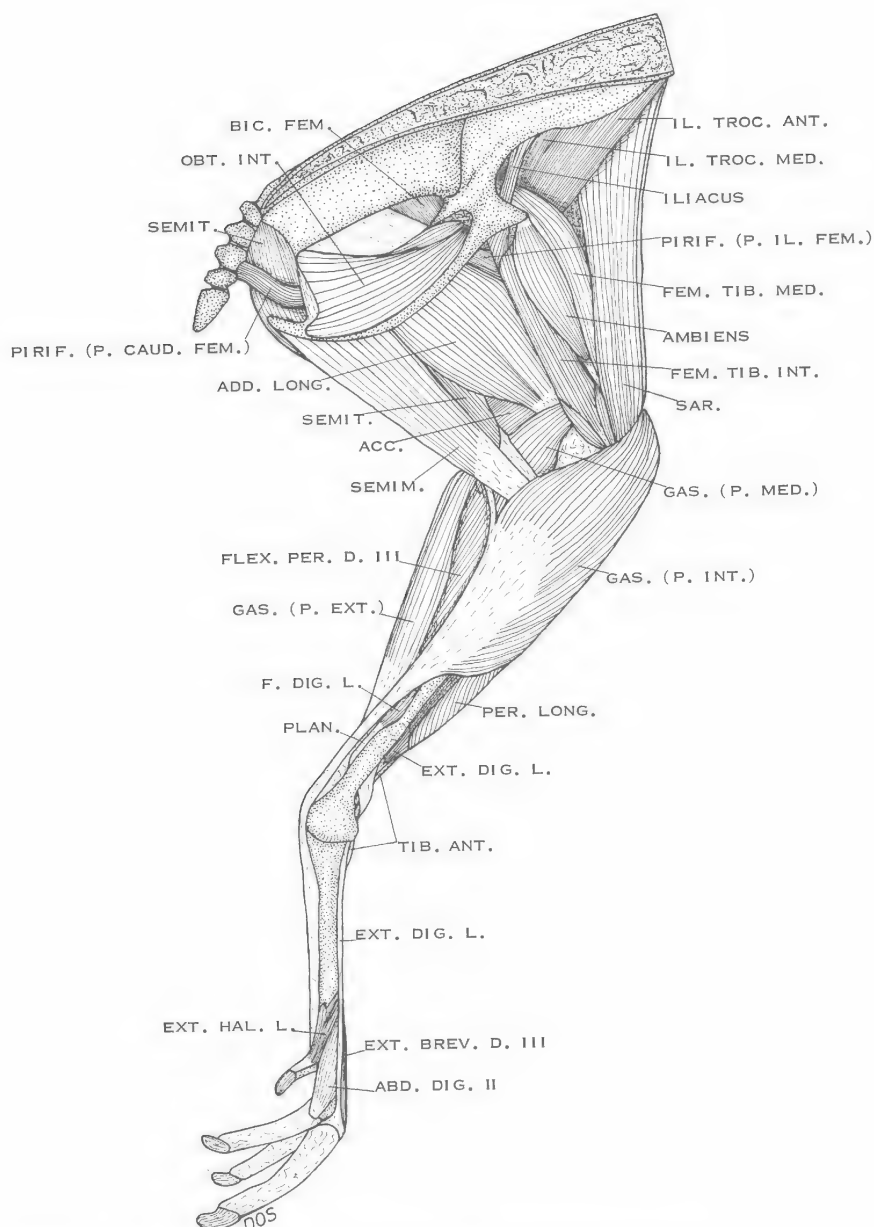


Figure 12. *Tinamus major*. Medial view of superficial muscles of the leg.

foratus muscles. It joins this tendon proximal to the Bic. fem. insertion, as in *Gallus* (Fig. 10).

M. sartorius (Sar.)

Similar in all, the origin mainly fleshy from the median ridge of the synsacrum and the anterior iliac crest. Belly strongly developed (Fig. 8); insertion mainly fleshy on the patellar tendon. The belly is firmly fused to the anterior edge of the Il. tib. proximally.

M. iliotibialis (Il. tib.)

The Il. tib. is very wide and strong as in *Gallus* (Fig. 8), extending from the Sar. posteriorly to the Semit., and concealing almost all of the underlying Bic. fem. The origin is by a thin, tendinous, sheet anteriorly, but arises fleshy from much of the posterior iliac crest. The fleshy part of the origin is least extensive in *Eudromia*, *Nothoprocta* and especially *Tinamotis*. The posterior border of the Il. tib. is fleshy all the way to the knee. The distal tendinous area is similar to *Gallus*. The insertion joins the Fem. tib. med. and Sar. to form the patellar tendon which inserts on the anterior tibial crest.

M. femoritibialis (Fem. tib.)

Femoritibialis externus (Fem. tib. ext.)

The belly is distinct and separate but enclosed by the more superficial Fem. tib. med. The origin is fleshy from the lateral surface of the femoral shaft, extending up to about the proximal third of that bone (Fig. 10); much longer in *Eudromia* (Table 2A, Item 206). The insertion is by an unusually narrow tendon on the lateral apex of the lateral cnemial crest of the tibia.

Femoritibialis medius (Fem. tib. med.)

Strongly developed and typical (Fig. 9). Lateral and medial heads separated by the insertion of the Il. troc. ant. The lateral head extends up to the Il. troc. post, and the medial head almost to the extreme proximal end of the femur. Insertion is on the internal and anterior tibial crests via the patellar tendon.

Femoritibialis internus (Fem. tib. int.)

The origin is fleshy from most of the medial surface of the shaft of the femur, extending up to the insertion of the Iliacus in all except *Tinamotis* (Fig. 13). Distally the posterior edge of the belly is more or less separate from the anterior part. Distally there is a superficial tendinous layer which is closely fused to the muscle. Insertion is by a narrow tendon on the medial tibial crest.

M. piriformis (Pirif.)

Pars caudifemoralis (P. caud. fem.)

Absent in *Eudromia*, present in all others. The origin is partly fleshy from the last two or three free caudal vertebrae in most specimens, with no connection to the pygostyle. The only attachment to the pygostyle was found in one leg of *Nothura darwini*. The vertebrae involved in the origin vary a great deal. In *Tinamus*, some *Crypturellus*, some *Nothoprocta*, and in *Tinamotis*, the last free caudal vertebra is not involved. The origin is from four free caudals in some *Nothoprocta*. The width

of the belly varies considerably, being narrowest in *Tinamus* and widest in *Nothura* (Table 2A, Item 209). Insertion is by a narrow tendon on the distal edge of the P. il. fem. in *Tinamus* and *Crypturellus* (except *C. tataupa*). The tendon of insertion is very short and the fusion with the P. il. fem. is very close to the femur in *Nothura* and *Nothoprocta*; intermediate in *Tinamotis*; fleshy to the femur in *C. tataupa* (Fig. 10).

Pars iliofemoralis (P. il. fem.)

Well developed in all, arising fleshy from the lateral surface of the ilium ventral to the posterior iliac crest and dorsal to the ilio-ischiatic fenestra. In addition to the main belly there is a small anterior head lying just posterior to the Glut. med. et min. and separated from the main belly by a bundle of nerves. The anterior edge of the muscle contains a small tendinous area as in *Gallus* in all except *Tinamus* and *Crypturellus*. In these the tendinous area is much larger, in some specimens extending clear across the muscle and dividing it into proximal and distal parts. The insertion is extensive and mainly fleshy on the posterior surface of the femur (Fig. 10).

M. semitendinosus (Semit.)

The origin is mostly fleshy from the posterior edge of the ilium and from the anterior caudal vertebrae. Both the Semit. proper and the Acc. Semit. are very strongly developed. Insertion on the tibia is by a flat tendon in common with the insertion of the Semim.

The length of the attachment of the Acc. Semit. to the femur is relatively shortest in *Tinamus*, *Crypturellus*, and *Tinamotis*; longest in *Nothoprocta*, reaching up to .46 femur (Table 2A, Item 214). The attachment to the femur is mainly fleshy, but in *Eudromia formosa* about the proximal half is tendinous.

The Semit. is strongly connected distally with the P. med. M. gas.

M. semimembranosus (Semim.)

The Semim. in *Tinamus* and *Crypturellus* arises fleshy from the pubis, with little or no connection with the ischium (Fig. 11); from the ventral edge of the ischium and adjacent pubis in all others, fleshy in all except *Nothoprocta* in which the origin is partly or entirely tendinous. Insertion is by a flat tendon on the tibia, in common with the Semit.

M. biceps femoris (Bic. fem.)

The origin is from a long, narrow, line on the posterior end of the anterior iliac crest and most of the posterior iliac crest, tendinous anteriorly, fleshy posteriorly (Fig. 9). *Tinamotis* differs slightly in having somewhat of a tendinous area at the posterior end of the origin.

Laterally the Bic. fem. is almost completely covered by the posterior part of the Il. tib. (Fig. 8). The belly is fleshy to the biceps loop and the tendon inserts as usual on a small tubercle on the fibula at .26-.35 Tib.-tar. (Fig. 10).

M. ischiofemoralis (Isch. fem.)

The origin is fleshy from most of the lateral surface of the ischium and the ventral part of the ilio-ischiatic membrane (Fig. 11). Insertion on the lateral

surface of the trochanter is by a short tendon which attaches just posterior to the insertion of the Glut. med. et min.

M. obturator internus (Obt. int.)

The Obt. int. arises fleshy from a large, triangular, area on the medial surface of the ischium, the ventral part of the ilio-ischiatic membrane, the ischio-pubic membrane and the adjacent edge of the pubis; attachment to the ilium is limited to a very small area located far posteriorly (Fig. 13).

The belly becomes narrow anteriorly and passes through the obturator foramen to the outside of the pelvis where it is closely attached to the Obt. ext. Insertion is by a thin, flat, tendon on the lateral surface of the trochanter. In *Tinamotis* the insertion is fleshy on the proximal edge.

M. obturator externus (Obt. ext.)

The Obt. ext. is single and fleshy throughout. It arises from the anterior and dorsal edges of the *F. obt.* and is closely attached to the Obt. int. Insertion is typical on the posterior surface of the femur, the point of attachment rather widely separated from that of the Obt. int.

M. adductor longus et brevis (Add. long.)

Origin of the Add. long. is from a long, narrow line on the ventral edge of the ischium and the adjacent pubis. The length of this area of origin varies from .24 (*Crypturellus*) to .34 (*Tinamus*, *Eudromia*) of the length of the femur. In most taxa the origin is mainly fleshy, but in *Tinamotis* the origin is tendinous posteriorly.

The belly is divisible more or less clearly into a P. ext. and a P. int. anteriorly in most; undivided posteriorly. In *Tinamotis* this division was discernible only distally; the division slight to none in *Nothura* and *Nothoprocta*.

Insertion is mainly fleshy on the posterior surface of the shaft of the femur. Posteriorly the distal edge of the muscle has a tendinous attachment to the medial edge of the medial head of the perforated flexors. The length of the femoral insertion varies considerably, being longest in *Nothura* and *Nothoprocta* and shortest in *Tinamus* (Table 2A, Item 301).

M. tibialis anterior (Tib. ant.)

The Tib. ant. is divided into the usual two parts, a larger, anterior head that arises fleshy from the anterior tibial crest, the extreme proximal end of the tibial shaft, and from the deep surface of the proximal portion of the belly of the Per. long.; and a smaller, posterior, head arising by a short tendon from the distal end of the external condyle of the femur. The two heads unite typically and the strong tendon passes under a heavy fibrous loop before inserting on the anterior surface of the Tar.-met. The tendon inserts by two very short branches, between which the Ext. pro. d. III extends proximally. The point of insertion is most proximal on the Tar.-met. in *Tinamus* and *Crypturellus*, most distal in *Tinamotis* (Table 2A, Item 327).

M. extensor digitorum longus (Ext. dig. l.)

The origin is fleshy from a long line on the antero-medial surface of the shaft of the Tib.-tar. Near the distal end of the shank the tendon passes under the fibrous

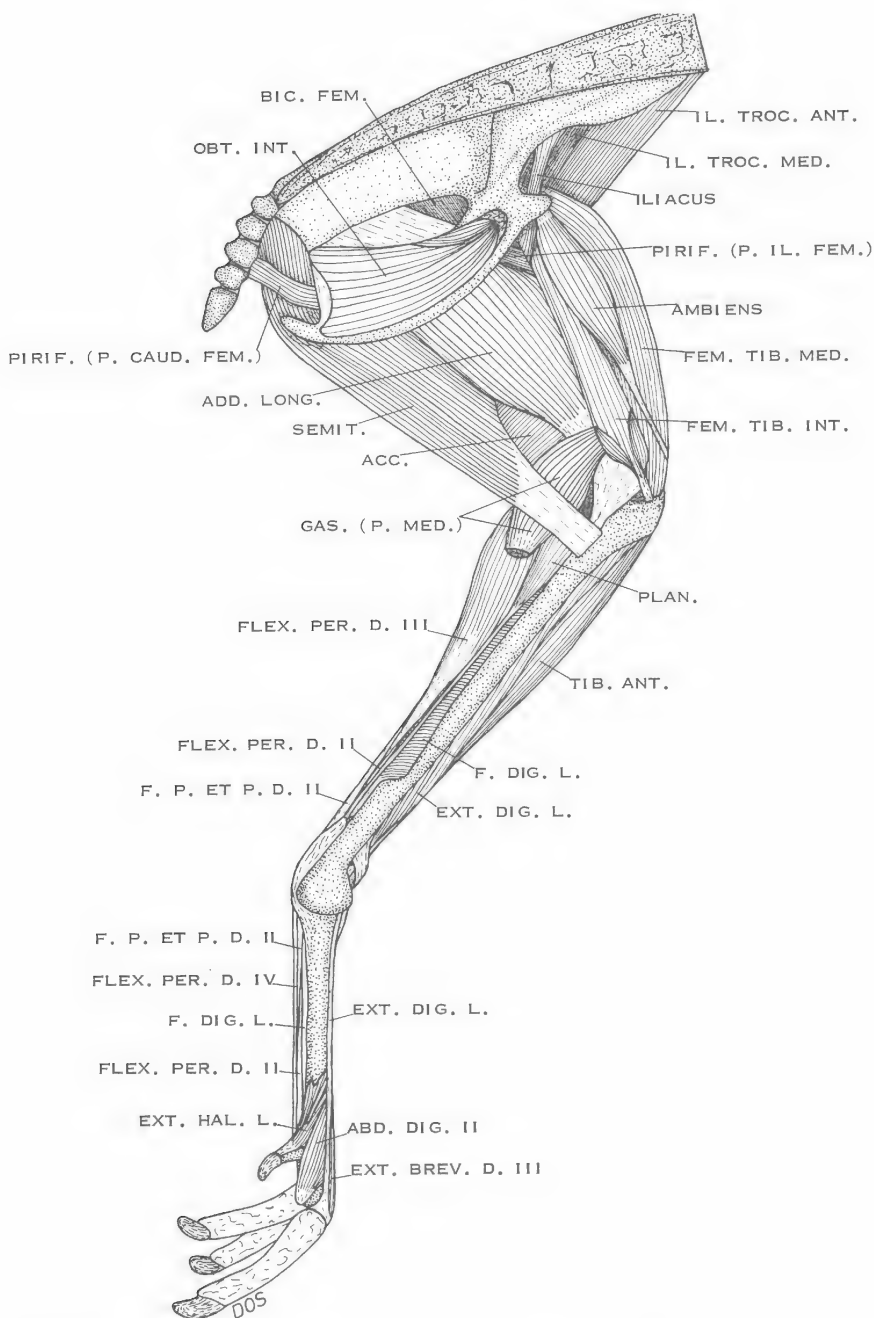


Figure 13. *Tinamus major*. Medial view of deeper muscles of the leg.

loop with the Tib. ant., then through the usual bony loop, then under a fibrous loop near the proximal end of the Tar.-met. The tendon bifurcates about midway the tarsus or below, but this point is subject to much individual variation (Table 4). Details of the complicated branching and points of insertion are given in Table 5 and shown in Fig. 14.

M. peroneus longus (Per. long.)

Belly wide, the origin tendinous on the medial side from a long, narrow, line on the tibia; laterally the origin is partly fleshy from a long area on the lateral surface of the fibula, and to a slight extent from the tibia distally in *Tinamus* and *Crypturellus*. The Per. long. forms a sheath around the Tib. ant. The tendon inserts on the lateral side of the tibial cartilage (Fig. 8) and on the tendon of the Flex. per. d. III as usual (Fig. 10). A short sesamoid is enclosed in the proximal part of the tendon in *Crypturellus* (except *C. tataupa*) but in no others.

M. peroneus brevis (Per. brev.)

Well developed in all except *Tinamotis* in which we could find no trace. The origin is typical, fleshy from a long line down the lateral side of the tibial shaft and adjacent fibula, beginning a little above the middle of the shank (Fig. 10). The short tendon passes under a tendinous loop at the base of the lateral malleolus of the Tib.-tar., and inserts on the proximal end of the Tar.-met. on the postero-lateral edge.

M. gastrocnemius (Gas.)

Divided into the usual three heads, all well-developed and typical. The P. int. extends around the front of the knee (Fig. 8). The P. ext. and P. int. have tendons that fuse distally (Table 2B, Item 303). The attachment of the P. med. to the P. int. is tendinous in *Tinamus* and *Crypturellus*, partly fleshy in others.

M. plantaris (Plan.)

The muscle is typical, with a short belly (Table 2B, Item 246) and with the insertion on the proximal end of the tibial cartilage on the medial side (Fig. 13).

M. flexor perforans et perforatus digiti II (F.p. et p.d. II)

The origin is fleshy from the tendinous origin of the P. ext. M. gas., from the lateral edge of the anterior surface of the patellar tendon and tendinous from the anterior surface of the anterior tendon or origin of the perforated flexors. The belly is short (Table 2B, Item 248), small, single, and slightly notched proximally. It lies directly posterior to the F.p. et p.d. III and is mostly covered by the P. ext. M. gas. (Figs. 8, 9). The tendon is broad and flat proximally, has a large dilation opposite Phal. 1, and inserts on the distal end of Phal. 1 and proximal end of Phal. 2.

M. flexor perforans et perforatus digiti III (F.p. et p.d. III)

The origin is fleshy from the tendinous origin of the P. ext. M. gas., from the lateral surface of the patellar tendon, and on the deep surface by a short tendon which arises from the antero-lateral edge of the tibial crest. The belly is much larger than the F.p. et p.d. II (Fig. 9). The tendon is flat proximally, has a large dilation

TABLE 4. Branches of the Extensor digitorum longus

	<i>Tinamus</i>	<i>Crypturellus</i>	<i>Nothoprocta</i>	<i>Nothura</i>	<i>Eudromia</i>	<i>Tinamotis</i>	
A. Medial branch							
To Digit II							
A1. To ungual Phal.	Yes	Yes	Yes	Yes	Only 1 tendon to Dig. II—to Phal. 2 and ungual	Yes	
A2. To base of Phal. 2	Yes	Yes	Yes	Yes		Yes	
To Digit III							
A3. Wide medial branch to base of Phal. 2	Yes	Yes—but sends narrow medial branch to ungual	About like <i>Crypturellus</i>	→			Yes
B. Lateral branch							
To Digit III							
B1. Medial branch to base of Phal. 3	Yes. Not fused to Ext. pro. d. III	Similar but more or less fused to Ext. pro. d. III	→			Fused to Ext. pro. d. III at base of Phal. 1—goes to 2, 3, 4 →	
To Digit IV							
B2. Medial branch to base of Phal. 3	Yes	Yes—but may extend to ungual	Yes	Yes	Absent	Yes	
B3. Medial branch to base of ungual	Yes	Yes	Yes	Yes	Yes	Yes	
B4. Lateral branch to base of Phal. 2	Yes	Yes	Yes	Yes	Yes	Yes	

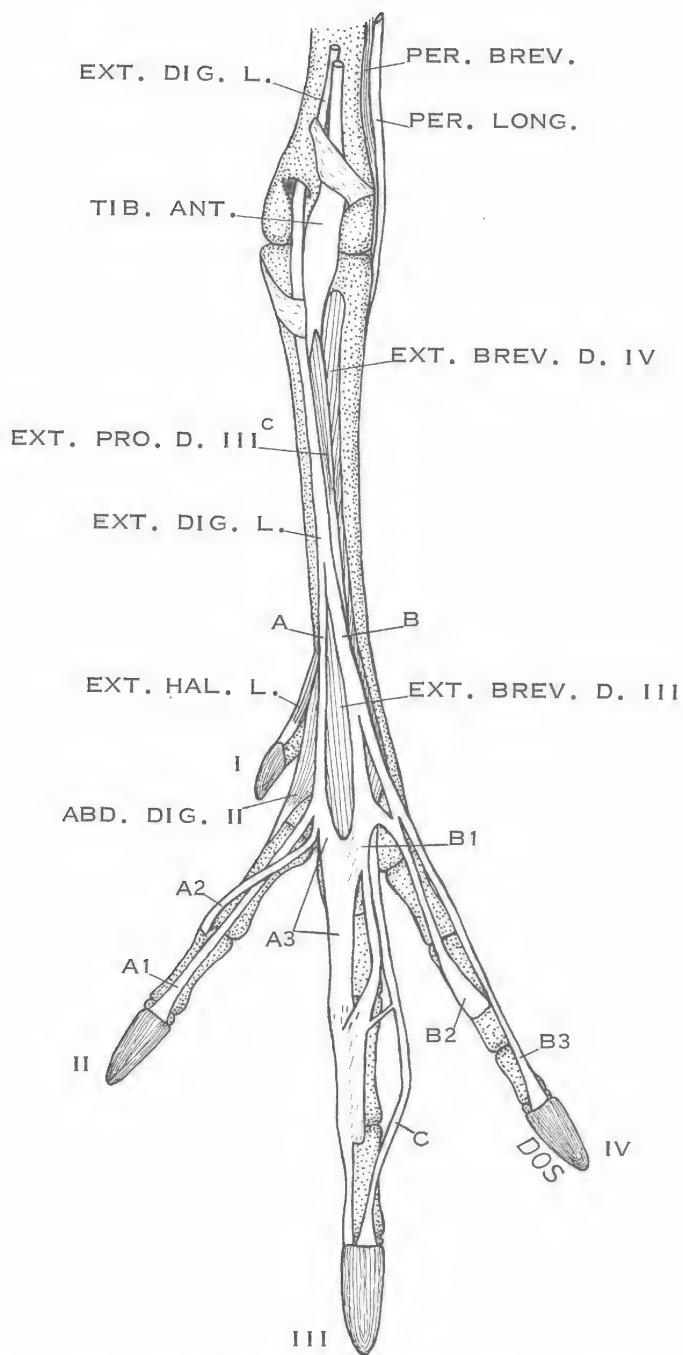


Figure 14. *Crypturellus tataupa*. Anterior view of superficial muscles of the foot.

opposite Phal. 1, and inserts on the distal end of Phal. 2 and the proximal end of Phal. 3.

M. flexor perforatus digiti II (Flex. per. d. II)

The origin is by two heads: a larger, medial head which arises mostly fleshy from the *Reg. intercon.* in common with the F. hal. 1. and the Flex. per. d. III and IV; and a much smaller, lateral, head which arises from a common tendon of the three perforated flexors. This tendon arises from the anterior and lateral surfaces of the proximal end of the fibula, and serves as the place of insertion of the Ambians. The Flex. per. d. II is deeply situated, lying directly posterior to the F. dig. 1. It is bounded laterally and posteriorly by the Flex. per. d. III. The tendon of insertion is dilated at the distal end of the Tar-met. It is perforated by the tendons of the F. dig. 1. and the F.p. et p.d. II and inserts on the proximal end of Phal. 1.

M. flexor perforatus digiti III (Flex. per. d. III)

The large medial head arises fleshy from the *Reg. intercon.* in common with the F. hal. 1. and the Flex. per. d. II and IV. The much smaller lateral head arises in common with the other two "perforatus" muscles as described for the Flex. per. d. II above. The two heads fuse without forming tendons and the belly forms a single tendon distally (Fig. 11). The Flex. per. d. III is the longest of the "perforatus" flexors, the belly ending at .71-.84 Tib-tar., with little variation among genera.

At the intertarsal joint the tendon of the Flex. per. d. III forms a sheath as usual, enclosing the tendons of the Flex. per. d. IV and F.p. et p.d. III. The tendon is dilated near the base of Phal. 1. Opposite Phal. 1 it is perforated by the tendons of the F. dig. 1. and F.p. et p.d. III, and inserts on the distal part of Phal. 1 and proximal end of Phal. 2.

The Flex. per. d. III is most peculiar in giving off at about .75 Tar-met., a small branch which has a fan-shaped insertion in the connective tissue over the bases of the proximal phalanges of digits II and III. This is present in all genera studied.

A short and typical vinculum is present near the distal end of the Tar-met. between the tendons of the F.p. et p.d. III and Flex. per. d. III in all genera (Fig. 11).

M. flexor perforatus digiti IV (Flex. per. d. IV)

The Flex. per. d. IV is the largest of the "perforatus" muscles. The large, medial head arises fleshy from the *Reg. intercon.* in common with the Flex. per. d. II and III; the smaller, lateral head arises in common with these two as described above. The two heads unite about midway the shank (Fig. 10), and the belly ends at .59-.72 Tib-tar.

The tendon is dilated near the base of Phal. 1, and opposite this phalanx it divides into four more or less distinct branches that insert as follows: (1) on the medial edge of the proximal end of Phal. 1; (2) on the distal end of 1 and the proximal end of 2; (3) on the distal end of the lateral edge of 2 and the proximal end of 3; and (4) on Phal. 3 and the proximal end of 4. In some *Crypturellus* branch "3" continues to the proximal end of Phal. 4, and in one *Nothoprocta* and in some *Crypturellus* branches "3" and "4" are fused.

M. flexor hallucis longus (F. hal. l.)

The F. hal. l. is small and deeply situated. The origin is fleshy from the *Reg.*

intercon. in common with the main flexor mass to which it is partly fused. The belly is shortest in *Tinamus* and *Crypturellus* and longest in *Nothoprocta*, *Nothura* and *Eudromia* (Table 2B, Item 269).

Below the middle of the tarsus the tendon fuses with that of the F. dig. I. in all except *Nothoprocta* and *Nothura*; in these the two tendons are connected by a short but wide vinculum (Gadow's Type II, 1891, p. 195). In *Tinamus* and *Crypturellus* the F. hal. I. gives off, just above the point of fusion with the F. dig. I., a branch to the hallux. In *Nothoprocta* and *Nothura* this branch comes off just proximal to the vinculum; however, in these the F. hal. I. tendon continues past the vinculum where it is continuous with the lateral head of the lumbricalis muscle. In the above four genera the branch to the hallux inserts on the ungual phalanx.

Eudromia and *Tinamotis* lack a hallux. In these the two deep flexors fuse and branches go only to the three fore-toes.

M. flexor digitorum longus (F. dig. I.)

The origin is fleshy from an extensive area on the posterior surface of the tibia and fibula; the belly notched proximally for the passage of nerves and blood vessels. The belly ends at .69-.89 Tib.-tar. Relationship of the tendon to that of the F. hal. I. is described above.

The trifurcated tendon sends a branch to the ungual phalanx of Dig. II, III, and IV. Small, elastic, slips extend from the tendons and insert on: Phal. 2 and 3, Dig. II; Phal. 2, 3, and 4, Dig. III; Phal. 2, 3, 4, and usually 5, Dig. IV. In some specimens the slip to Phal. 2, Dig. IV was not found.

A short sesamoid was found in the tendon just proximal to the trifurcation in *Crypturellus soui*; absent in all others.

M. popliteus (Pop.)

Present in all, with some variation in shape. Quadrangular in *Tinamus* and *Crypturellus*; more or less triangular in others, the narrow origin from the fibula more or less tendinous.

M. extensor hallucis longus (Ext. hal. I.)

Absent in *Eudromia* and *Tinamotis*, conforming to the lack of a hallux. In other genera the Ext. hal. I. usually consists of two parts: a long, slender, head arising fleshy from the medial side of the anterior metatarsal groove; a short, stout, head arising from the medial surface of the Tar.-met. just proximal to the hallux, and from Met. I (Fig. 15). The proximal head is vestigial or absent in four legs of *Crypturellus soui*.

The entire muscle is shortest in *Tinamus* and most *Crypturellus*, much longer in *Nothoprocta* and *Nothura* (Table 2C, Item 340). The tendon of the proximal head is much longer in the latter two.

The two heads merge distally and the common tendon inserts on the ungual phalanx of the hallux.

M. extensor brevis digiti III (Ext. brev. d. III)

The origin is fleshy from about the distal half or third of the anterior surface of the Tar.-met., located between the Abd. dig. II and the Ext. brev. d. IV (Fig. 15). Insertion is by a short, flat, tendon on the antero-proximal edge of Phal. I., Dig. III.

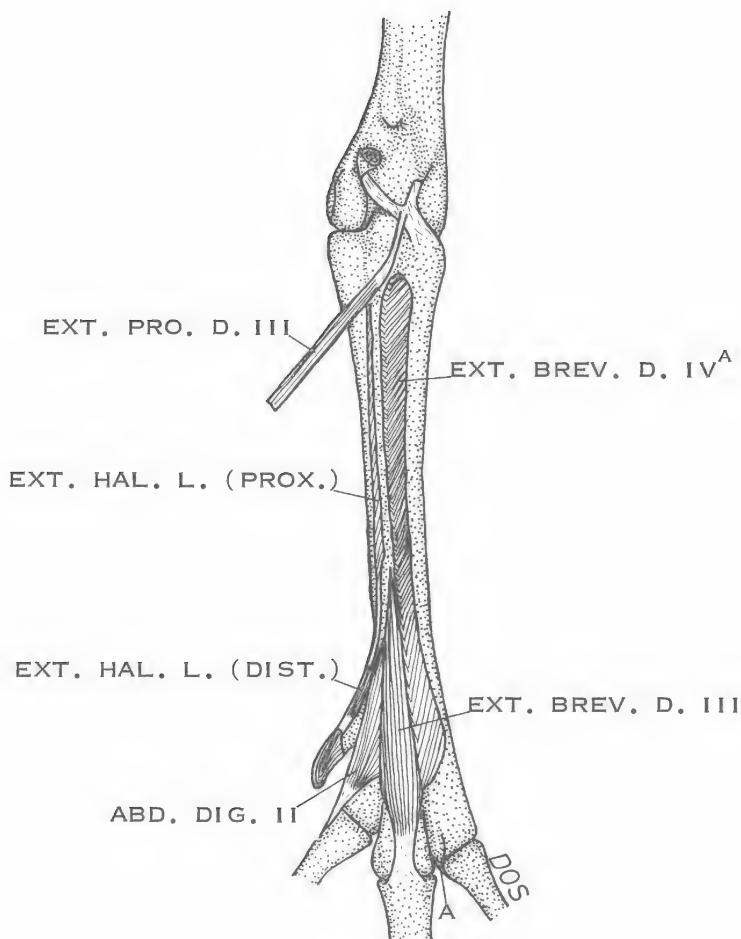


Figure 15. *Crypturellus tataupa*. Anterior view of deep muscles of the foot.

M. extensor proprius digiti III (Ext. pro. d. III)

The origin is by a short tendon from the anterior surface of the intertarsal joint capsule, between the distal malleoli of the Tib-tar. At the point of origin the tendon is attached to a roundish swelling that consists of fibro-cartilage in some, but is ossified in some, forming a small sesamoid (Table 4).

The Ext. pro. d. III perforates the tendon of the Tib. ant. and extends distally along the lateral surface of the tendon of the Ext. dig. I. (Fig. 14). There is considerable variation in the length of the belly (Table 4). In one leg of *Eudromia* only, the belly has a long, fleshy, origin from the anterior midline of the Tar-met.

In *Tinamus* the tendon passes between the distal ends of Met. III and IV, thence along the antero-lateral surface of Dig. III to the insertion on the base of the unguis phalanx, seemingly replacing that attachment of the Ext. dig. I. which terminates on

the base of Phal. 3. In some genera the tendon is more or less fused with that of the Ext. dig. I. In *Eudromia* and *Tinamotis* this fusion is complete at the base of Phal. 1 (Table 5).

M. extensor brevis digiti IV (Ext. brev. d. IV)

The origin is typical and fleshy from most of the length of the antero-lateral surface of the Tar-met. (Fig. 15). The tendon passes through a bony canal in the outer inter-metatarsal space and inserts on the medial edge of Phal. 1, Dig. IV, thus serving as an abductor.

M. abductor digiti II (Abd. dig. II)

The short, stout, belly arises fleshy from the medial and antero-medial surface of the Tar-met. A few fleshy fibers are usually attached to Met. I. The muscle is longest in *Tinamus*, extending up to .56(.51-.59) Tar-met.; somewhat shorter in most. Insertion is by a short tendon on the medio-proximal edge of Phal. I, Dig. II (Fig. 15).

M. flexor hallucis brevis (F. hal. brev.)

Absent in *Eudromia* and *Tinamotis* which lack the hallux; present and single throughout in all others. The origin is fleshy from a long, narrow, line on the medial edge of the posterior surface of the Tar-met. The muscle is much longer in *Nothoprocta* and *Nothura* than in *Tinamus* and *Crypturellus* (Table 2C, Item 353). Insertion is by a short tendon on the base of the hallux.

M. adductor digiti II (Add. d. II)

The Add. d. II is present in all except *Tinamotis* in which we could find no trace. The origin is fleshy from the posterior surface of the Tar-met. The muscle is narrow proximally, much wider distally, and is confined to the distal half or less of the Tar-met. (Fig. 16). Insertion is by a short tendon on the lateral edge of Phal. 1, Dig. II.

M. lumbricalis

In most genera the origin is typical, from the anterior surface of the trifurcated deep flexor tendon. The muscle is usually divided into two more or less distinct parts, a large medial and a smaller lateral head. The medial head inserts on the joint pulley for Dig. III, the lateral head on the pulley for Dig. IV.

Nothoprocta and *Nothura* are peculiar in that the lateral head arises as a direct continuation of the distal end of the F. hal. I. tendon. In *Nothura* the lateral head inserts as a shiny tendon, less distinctly so in *Nothoprocta*. The insertion appears fleshy in others.

M. abductor digiti IV (Abd. d. IV)

Typical, the origin fleshy from a long, narrow, line along the postero-lateral edge of the Tar-met. (Fig. 16). Insertion is by a short tendon on the latero-proximal edge of Phal. 1, Dig. IV.

M. adductor digiti IV

We found no trace of this muscle which was described by Gadow (1891, p. 204).

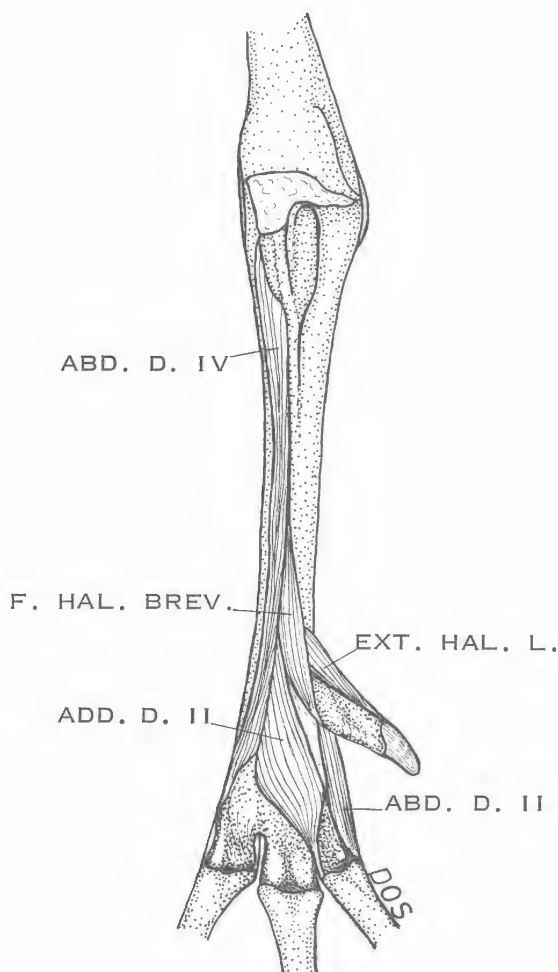


Figure 16. *Crypturellus tataupa*. Posterior view of tarsus showing short foot muscles.

Synopsis of the More Interesting Features of the Appendicular Muscles of Tinamous

The following brief resumé considers the myological features of appendicular muscles that show important differences between various groups of birds. Any muscles not listed are present in tinamous and do not exhibit any unusual structure.

Lat. dor. post.—The origin is unusually extensive, being partly from thoracic ribs: 2, 3, 4, 5 in *Tinamus* and *Crypturellus*; 4, 5 in other genera.

Cor. bra. ant.—Instead of a short muscle as in most birds, tinamous have, in addition, an enormous distal extension with a fleshy insertion over most of the anterior surface of the humerus.

Delt. min.—The belly of the long head is completely fused for most of its length with the belly of the Sup. cor.

Biceps slip—Absent in all.

Exp. sec.—The small, distal, head arising from the internal epicondyle is present but almost

- vestigial. The proximal head attached to the axillary tendon is well developed; this tendon is attached to the Lat. dor. post. and Scap. hum. post., and has two strong branches proximally, one from the sternum and one from the scapula.
- Ent. ul.—Well developed in all.
- F. dig. prof.—The tendon sends a strong branch to the pollex.
- E. meta. rad.—A partial division of belly, otherwise single.
- E. dig. com.—Sends a short branch to the pollex.
- E. pol. 1.—Two-headed; tendon fused with E. meta. rad. at wrist.
- E. ind. 1.—Distal head present in all genera except *Eudromia* and *Tinamotis*.
- Ul. meta. dor.—A small dorsal head and a large ventral head; only slight attachment to quills; ventral head absent in *Tinamotis*.
- E. pol. br.—Arises from the common tendon of the E. meta. rad. and E. pol. 1., with usually no, sometimes a slight, connection with the Car. met.
- Abd. pol.—Single, origin fleshy from tendon of E. meta. rad.
- Int. dor.—Tendon divided opposite Phal. 1 into an anterior and a posterior branch. At the base of Phal. 2 a vinculum connects the posterior tendon with the tendon of the Int. vol.
- Il. troc. med.—Fused with Il. troc. ant. in *Tinamus* and *Crypturellus*; separate in other genera, with some exceptions.
- Glut. med. et min.—Present in all.
- Ambiens.—Well developed in all.
- Il. tib.—Very wide and strong, the origin extending from the Sar. to the Semit.
- Fem. tib. ext.—Well developed and distinct, the insertion by a narrow tendon.
- P. caud. fem. of Pirif.—Absent in *Eudromia*, present in all others, the origin from free caudal vertebrae; usually no connection with the pygostyle.
- P. il. fem. of Pirif.—Well developed in all. A small anterior head is separate proximally from the main belly.
- Semit.—Both main belly and Acc. well developed in all. Origin from proximal caudal vertebrae and posterior edge of ilium. The insertion is by a common tendon with the Semin.
- Obt. int.—Large, triangular, attached to ilium on a small area posteriorly.
- Obt. ext.—Single, fleshy, the insertion separate from the Obt. int.
- Add. long.—Divided into a P. ext. and P. int. anteriorly in some; little or no division in some.
- Ext. dig. 1.—The tendon bifurcates about midway the tarsus or a little below.
- Per. long.—Origin includes a long, fleshy, attachment to fibula; insertion typical.
- Per. brev.—Absent in *Tinamotis*; typical in all others.
- Gas.—Three-headed. The P. int. extends around front of knee. P. int. and P. ext. have separate tendons that fuse above heel.
- Plan.—Typical.
- F. p. et p. d. III.—The origin is partly from a short tendon from the lateral edge of the tibial crest; no fleshy connection with fibula.
- Flex. per. d. III.—The two heads form a single tendon distally. At about .75 Tar.-met. the tendon sends off a small branch that fans out over the bases of digits II and III.
- Vinculum.—Typical, between the F. p. et p. d. III and Flex. per. d. III in tarsus.
- Flex. per. d. IV.—A large medial and small lateral head. The tendon is divided opposite Phal. 1 into four more or less distinct branches that insert on phalanges 1-4.
- F. hal. 1.—Belly small and deeply situated. The tendon fuses in the tarsal region with the F. dig. 1. in all except *Nothoprocta* and *Nothura*. In these the two are connected by a vinculum. A branch goes to the hallux in all except *Eudromia* and *Tinamotis* which lack this digit.
- Popliteus.—Present in all.
- Ext. hal. 1.—Consists, when present, of a proximal and a distal head in all except some *Crypturellus*. Absent in *Eudromia* and *Tinamotis*. Insertion is on the ungual phalanx.
- Ext. brev. d. III.—Short, confined to the distal third or half of the tarsus.
- Ext. pro. d. III.—Arises from the intertarsal joint capsule; perforates the tendon of the Tib. ant. The tendon inserts on the ungual phalanx in some, but fuses with the branch of the Ext. dig. 1. to the middle toe in others.
- Ext. brev. d. IV.—Typical, the origin from most of the tarsal length.
- Abd. dig. II.—Well developed.
- F. hal. brev.—Present and single in those genera with a hallux. Absent in *Eudromia* and *Tinamotis*.
- Add. d. II.—Confined to distal half or less of the tarsus, the tendon short. Absent in *Tinamotis*.
- Lumbricalis.—Usually divided into two more or less distinct parts.
- Abd. d. IV.—Typical, the origin from most of the tarsal length.
- Sesamoids.—Following are the only ones found:
- Per. long.—A short sesamoid in the proximal part of the tendon in *Crypturellus* only, but absent in *C. tataupa*.
- F. dig. 1.—A short sesamoid in the distal end of the tendon, just proximal to the trifurcation, in *Crypturellus soui* only.
- Ext. pro. d. III.—A rounded dilation in the anterior surface of the intertarsal joint capsule serves as the point of origin of the Ext. pro. d. III. This is ossified in *Nothoprocta* and *Eudromia*, and in some *Crypturellus* and *Nothura*. Not ossified in *Tinamus* and *Tinamotis*.

Discussion and Conclusions

Tinamous have generally been considered to be one of the most primitive groups of living birds, showing affinities with the Ratitae and the Galliformes (Alix, 1874; Gysels, 1970), with the Ratitae only (Parkes, 1966). Their divergence was sufficiently early, and adaptive radiation sufficiently great, to mask most of the morphological clues to their derivation. Tinamous show a number of interesting myological characters that differ from the muscles of other birds, and which suggest, along with other morphological characters, that tinamous probably existed as a distinct group for a long period. Brodkorb (1963) refers to the Tinamidae in the late Pliocene. The primitive nature of tinamous is confirmed by the appendicular musculature, the biceps slip being the only muscle absent in all forms studied. However, the P. caud. fem. is absent in *Eudromia*, the Per. brev. and Add. d. II in *Tinamotis*. Both *Eudromia* and *Tinamotis* lack the distal head of the E. ind. I. and since they lack the hallux, the Ext. hal. I., F. hal. brev., and the deep flexor tendon to this digit are also absent.

The following muscles of tinamous differ from the condition found in most birds, but resemble that of one or more ratite birds, and perhaps thus qualify as representing the primitive condition.

Cor. bra. ant.—The distal part extends far out on the humerus to the brachialis muscle. According to Fürbringer (1902, p. 455) this muscle is also large in *Struthio* and *Rhea*, but he considered this similarity without significance. Hoff (1966) found a considerably enlarged Cor. bra. ant. in owls.

Ent. ul.—Present only in Galliformes (not *Opisthocomus*), tinamous, and we have confirmed its presence in *Apteryx* (George and Berger, 1966, p. 354).

F. dig. prof.—Sends a branch to the pollex. Few other birds show this condition: *Heliornis*, *Struthio* (Gadow and Selenka, 1891, pp. 280-81), *Odontophorus*, *Opisthocomus* (Hudson and Lanzillotti, 1964, p. 25), and owls (Hoff, 1966).

P. caud. fem.—Origin from free caudal vertebrae, usually no connection with the pygostyle. The origin from free caudal vertebrae has been reported in the Ratitae (Gadow and Selenka, 1891, p. 158). We have found the origin in *Struthio* from several anterior caudal vertebrae and in *Apteryx* from the pygostyle and the last free caudal vertebrae. Wilcox (1952, p. 523) reported the origin in *Gavia* as from the "coccygeal vertebrae." Specimens of *Gavia immer* we have examined have the origin from the fascia on the ventral surface of the pygostyle as in many birds.

P. il. fem.—A small anterior head is separated from the main belly by the sciatic nerve and artery. This condition is found only in the Ratitae and tinamous (Garrod, 1881, p. 206, Fig. 6).

Ext. pro. d. III.—This muscle is of constant occurrence in tinamous, and we have found it in the five living genera of Ratitae. In other orders of birds the Ext. pro. d. III is of rare and irregular occurrence. Gadow (1880, p. 54) called this the extensor longus digiti III and figured it for *Rhea*. The description given for the two short extensors to the third toe by Gadow and Selenka (1891, pp. 199-200) was badly garbled. The terminology has been clarified by Holmes (1962, p. 485).

The most peculiar features of the appendicular musculature that we have found in all tinamous examined are restricted to the wing:

Lat. dor. post.—The large size of this muscle and its extensive origin, which includes attachment to one or more ribs, is a condition we have observed only in some of the diving birds such as loons, auks, and penguins.

Cor. bra. ant.—The enormous size of this muscle far exceeds that found in any other group of birds.

Delt. min.—The ventral or long head is firmly fused throughout most of its length with the belly of the Sup. cor.

E. pol. br.—The origin is from the common tendon of the E. meta. rad. and E. pol. l., with little or no attachment to the carpometacarpus.

Int. dor.—The double tendon of insertion and the vinculum connecting the tendon of the Int. dor. to the tendon of the Int. vol. near the base of Phal. 2, Dig. II (III) are features we have observed only in tinamous.

We consider it likely that the exceptionally strong development of the Lat. dor. post. and the Cor. bra. ant. is linked in some functional way, correlated with the manner of flight in tinamous. These birds may have evolved in an arid scrub habitat where escape from ground predators involved flying up at a very steep angle to avoid the dense vegetation before leveling off in horizontal flight. A detailed analysis of the manner of flight in tinamous still inhabiting dense scrub might yield interesting results.

Our numerical comparisons show (Fig. 17) that the forest-dwelling *Tinamus* and *Crypturellus* are very closely related. One can argue that the similarity of these two genera is a result of convergence, but since so many muscle characters were used in the analysis this appears unlikely, especially since studies of other parameters confirm our conclusions. Osteological comparisons of a number of species of these two genera reveal few significant qualitative or quantitative differences (Lancaster, unpubl.). Plumage patterns, quality of call notes, and egg color also exhibit likenesses that they do not share with other tinamous.

Tinamus and *Crypturellus* agree in several muscle characters that differ from the

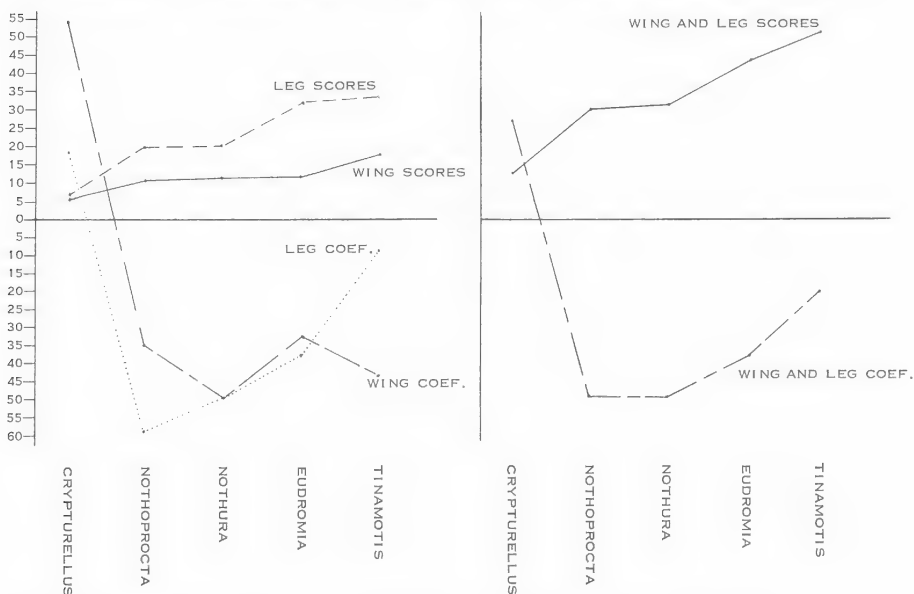


Figure 17. Wing and leg scores and coefficients comparing *Tinamus* to other genera.

conditions found in other genera: the Lat. dor. post. has a more extensive origin, including parts of thoracic ribs 2 and 3, and separates the origins of the Serr. sup. met. and Serr. sup. post; the supinator is distinctly longer; the ventral head of the Ul. meta. dor. is very large; the Il. troc. ant. and med. are fused in all specimens; the tendinous area in the belly of the P. il. fem. is very large; the bellies of the F. hal. l., Ext. hal. l., and F. hal. brev. are very short.

Besides mostly small differences in measurements of various muscles (Tables 1, 2), *Tinamus* and *Crypturellus* show a few qualitative differences: insertion of the Serr. sup. ant. is mainly posterior to the origin of the P. ext. M. subscp. in *Tinamus*; the distal head of the E. ind. l. is sometimes absent in *Tinamus*; the ambiens arises by a short tendon in *Tinamus*, partly fleshy in *Crypturellus*; the medial branch of the Ext. dig. l. to digit III inserts on Phal. 2 in *Tinamus*, on Phal. 2 and the ungual in *Crypturellus*; there is a sesamoid in the Per. long. in *Crypturellus*, not in *Tinamus*.

The one forest genus not considered in this study is *Nothocercus*. Osteologically, it appears close to *Tinamus* and *Crypturellus*, but not as close as the latter two genera are to each other.

Nothoprocta and *Nothura* inhabit the open and semi-open country of the central and southern Andes, and most of the continent south of the Amazon Basin. These genera are obviously closely related, with lower leg and wing scores than even *Crypturellus* and *Tinamus*. Again, their skeletons, ecology, egg color, and plumage patterns share similarities that substantiate the conclusions reached by our investigation of myology.

Nothoprocta and *Nothura* share few myological characters that are lacking in other tinamous. Notable exceptions are the presence of a vinculum between the tendons of the F. hal. l. and F. dig. l., and the very peculiar origin of the lateral head of the

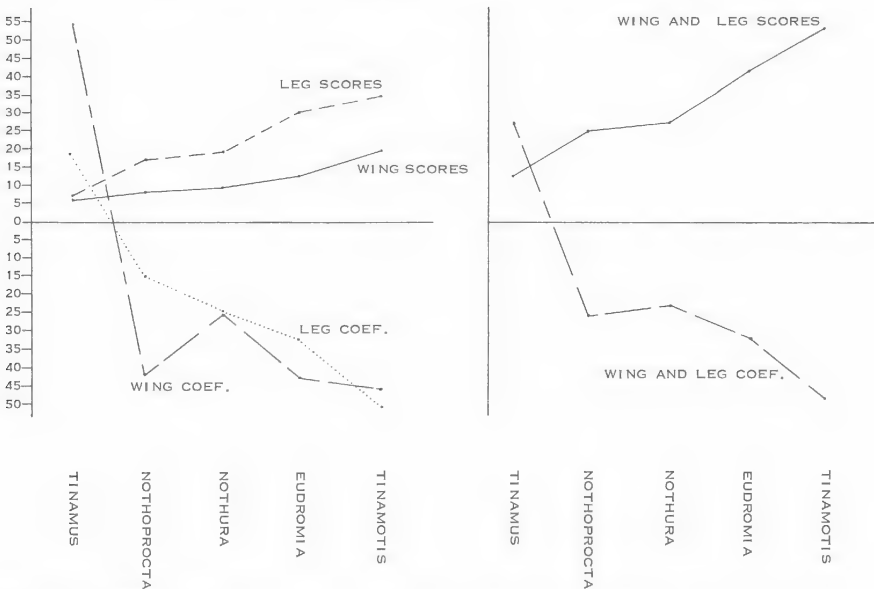


Figure 18. Wing and leg scores and coefficients comparing *Crypturellus* to other genera.

lumbricalis—which arises from the distal end of the F. hal. l. tendon. Only trivial differences were noted between these genera.

Our cumulative scores indicate that *Nothoprocta* and *Nothura* are somewhat closer to *Tinamus* and *Crypturellus* than to *Eudromia* and *Tinamotis*; the correlation coefficients do not confirm this (Figs. 19, 20).

The monotypic genus *Taoniscus* was unobtainable for dissection, but the plumage, osteology, and what little is known about the ecology strongly suggest a close affinity with *Nothura* and *Nothoprocta*, although probably not as close as the latter two genera are to each other.

Rhynchotus, also a monotypic genus, and one that we could not obtain for dissection, inhabits grasslands and savannas south of the Amazon. While it seems to be a distinctive genus, we cannot substantiate, on the basis of myology, whether it is most closely related to *Nothura* and *Nothoprocta* as indicated by its osteology, ecology, and egg color.

Eudromia and *Tinamotis*, adapted to the more arid and open steppes and the high Andes, show the greatest degree of specialization of the appendicular muscles. They have lost the hallux and all trace of muscles associated with it.

Our results indicate that *Eudromia* is not very similar to other genera studied (Fig. 21), but is closer to *Nothura* and *Nothoprocta* than to *Tinamus* and *Crypturellus*, and appears closest to *Tinamotis*. The only unique features we found in *Eudromia* are:

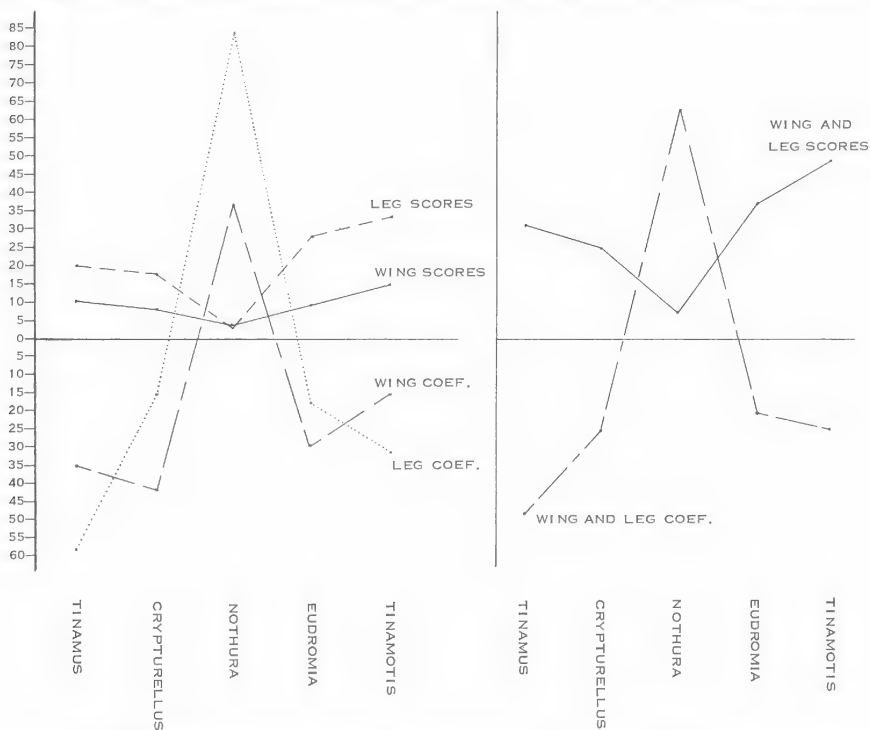


Figure 19. Wing and leg scores and coefficients comparing *Nothoprocta* to other genera.

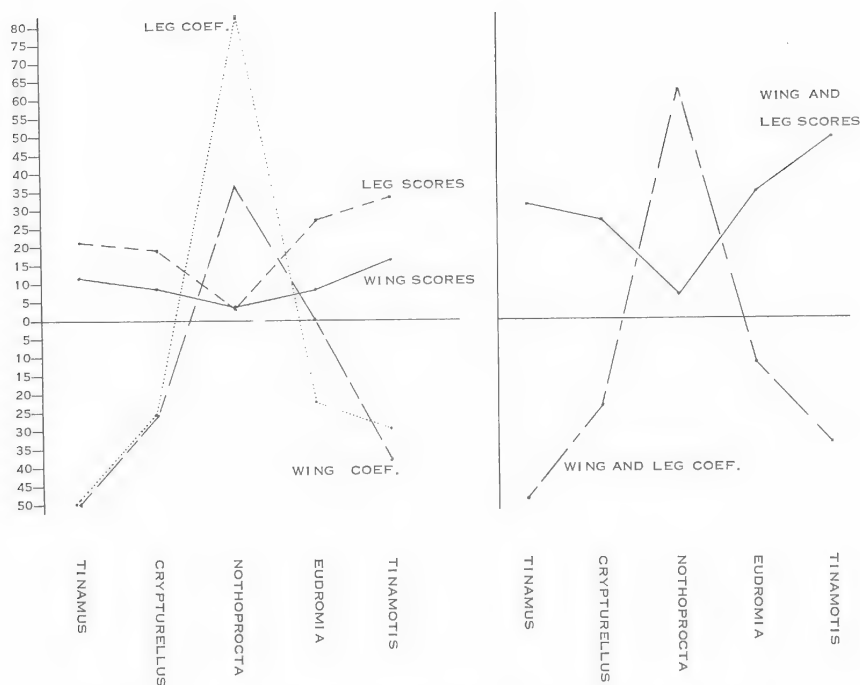


Figure 20. Wing and leg scores and coefficients comparing *Notthura* to other genera.

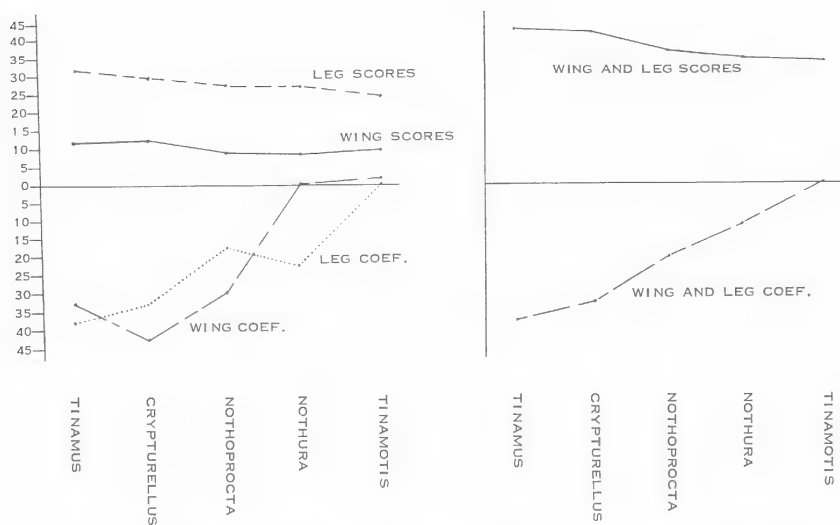


Figure 21. Wing and leg scores and coefficients comparing *Eudromia* to other genera.

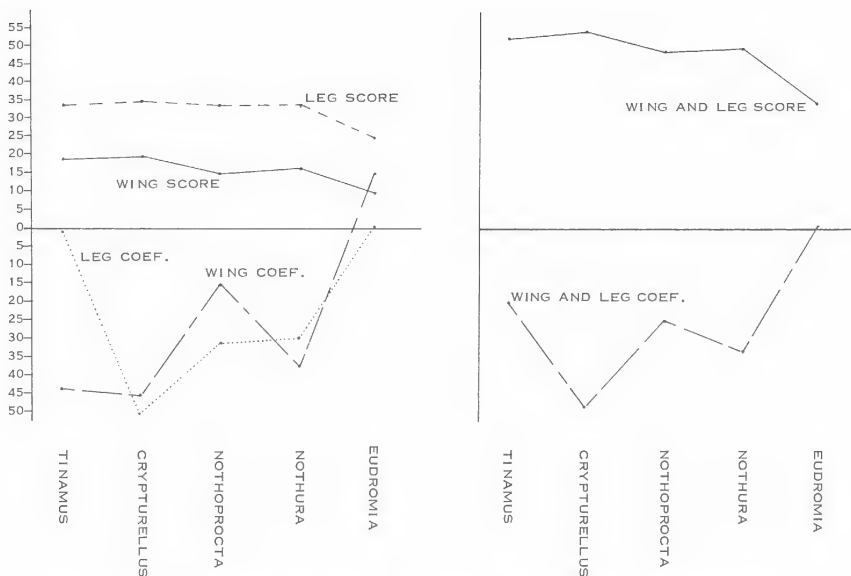


Figure 22. Wing and leg scores and coefficients comparing *Tinamotis* to other genera.

absence of the P. caud. fem.; only one branch of the Ext. dig. I. to digit II and only two branches to digit III (Table 2).

The only features shared by *Eudromia* and *Tinamotis* that were not found in other genera are: distal head of the E. ind. I. absent (absent in one *Tinamus*); lateral branch of the Ext. dig. I. to digit III firmly fused to the tendon of the Ext. pro. d. III. The principal source of agreement of these two genera is the absence of the hallux and the muscles involved. This suggests that the loss of this digit might be a case of convergence, rather than indicating a common ancestry.

Among the tinamous studied *Tinamotis* is clearly the most specialized in the appendicular musculature. It has not only lost the muscles and tendons for the hallux, but is unique in the absence of the ventral head of the Ul. meta. dor., the Per. brev., and the Add. d. II.

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A Species of the Genus *Eunice* (Polychaeta) from the Pacific Northwest Coast

Introduction

The polychaete genus *Eunice* Cuvier, 1817, contains 146 taxonomically valid species (Fauchald, 1970). Utilitarian subdivisions of the genus were suggested by Hartman (1944) based on the color and dentition of the subacicular hooks, and by Fauchald (1970) based on the distribution of the branchiae.

One group of *Eunice* species presenting considerable taxonomic difficulty has yellow, bidentate subacicular hooks and branchiae first present before setiger 10 and present not further back than setiger 100. Six species (*E. biannulata* Moore, 1904; *E. kobeensis* McIntosh, 1885; *E. segregata* Chamberlin, 1919a; *E. semisegregata* Fauchald, 1970; *E. valens* Chamberlin, 1919b; and *E. websteri* (Webster, 1884)) of this group occur on the northwest coast of North America and have been redescribed by Fauchald (1969). Both the original descriptions of these six species and the revised descriptions by Fauchald are based on type and paratype specimens only. Most of these specimens are in poor condition; about half of them are posteriorly incomplete. Furthermore, there is no published account of the amount of morphological variation present in any population of any of these species of *Eunice*, and therefore the suggested diagnostic species characters (Fauchald, 1969, and previous workers) are primarily subjective.

The present report contains a morphological analysis of 90 specimens of *Eunice* from the intertidal area of the San Juan Archipelago in the state of Washington, two specimens from the intertidal near Victoria, B.C., and 25 specimens from subtidal stations off Amchitka Island, Alaska (for precise locations of specimens see Table 1).

Results and Discussion

A total of 19 morphological characters are analyzed; not all characters are analyzed for all specimens. Many of these characters are essentially qualitative; these are discussed first. Quantifiable characters are analyzed statistically and are discussed in the second half of this report.

Qualitative Characters

The five prostomial (occipital) tentacles of *Eunice* can be either smooth or articulated. Articulated tentacles can have either cylindrical or moniliform articles. All of the specimens examined have essentially cylindrical tentacular articles; however, there was a tendency for the articulations to become progressively more moniliform distally, especially in the outermost tentacles. This character seems to have been confused

TABLE 1. Locations of the specimens analyzed in this report. The animals were obtained at various times from 1968 to 1971.

Specimen Number	Locality	Latitude	Longitude	Depth
	San Juan Archipelago			
1-68	Turn Point, San Juan Island	48° 32.1' N	122° 58.4' W	low intertidal
69-80	Iceberg Point, Lopez Island	48° 25.3' N	122° 53.6' W	low intertidal
81-90	Mitchell Bay, San Juan Island	48° 34.1' N	123° 10.4' W	low intertidal
	Victoria, British Columbia			
91-92	Esquimalt Lagoon	48° 25.8' N	123° 27.2' W	low intertidal
	Aleutian Islands, Alaska			
93	Makarius Bay, Amchitka Island	51° 23' N	179° 13' E	6 meters
94-103	Bering Sea, near Rat Islands	51° 30' N	179° 16' E	180 meters
104	Constantine Harbor, Amchitka Island	51° 24' N	179° 18' E	35 meters
105	Pacific Ocean, near Rat Islands	51° 19.3' N	178° 55' E	270 meters
106-107	Pacific Ocean, near Rat Islands	51° 19.5' N	179° 02' E	180 meters
108-110	Bering Sea, near Rat Islands	51° 29.2' N	179° 17.3' E	210 meters
111-117	Off Amchitka Island	51° 31.5' N	179° 16' E	180 meters

in the literature, partly because it is difficult to know how constricted the articulations need to be before the tentacles can be termed moniliform. Hartman (1944) has stated that the form of the prostomial tentacles "cannot be taken as [a criterion] for speciation."

The Alaskan specimens had very smooth nuchal cirri $\frac{1}{2}$ -one times the length of the "peristomium."¹ The nuchal cirri of the San Juan and Victoria specimens were usually equal to the "peristomium" in length and had up to five-seven faint articles, but many specimens, especially the smaller ones, were perfectly smooth.

Fauchald (1969) stated that the dorsal cirri of anterior setigers can be either smooth or articulated, and used this as one of the diagnostic characters for separating the six species in question. The cirri on the majority of the specimens here examined are very smooth (Fig. 1-b), but in many specimens a variable degree of crumpling could be seen giving the impression of faint articulations.

The parapodial lobes in the branchial region are believed to be species specific in shape (Fauchald, 1969). Upon a reexamination of the holotype of *E. kobiensis* (British Museum of Natural History specimen #1885:12:1:197), it is the author's opinion that the parapodia near setiger 28 are not like those drawn by Fauchald for *E. kobiensis* (1969), but are indistinguishable from the figure given by McIntosh for the twentieth parapodium of the holotype (1885). There is some variation in this character, but most specimens here examined resemble McIntosh's drawing.

The second parapodia of the present material (Fig. 1-b) resemble that shown for *E. kobiensis* by Fauchald (1969), but since similar drawings are not shown for all six species, comparisons are not possible.

The form of the setae is fairly constant. Figure 2 shows a subacicular hook, a comb seta, and a compound falciger of a specimen from the San Juan Islands.

¹Traditionally, the "peristomium" of *Eunice* is a long ring immediately posterior to the prostomium and anterior to the apodous ring bearing the nuchal cirri dorsally. Akesson (1967) has shown from an embryological analysis that the "peristomium" and nuchal ring are both presegmental subdivisions of the head, and therefore the use of the term "peristomium" is misleading because it implies that it is homologous with the peristomium of other polychaetes. Like Akesson, I use quotation marks to signify that this term is inapt.

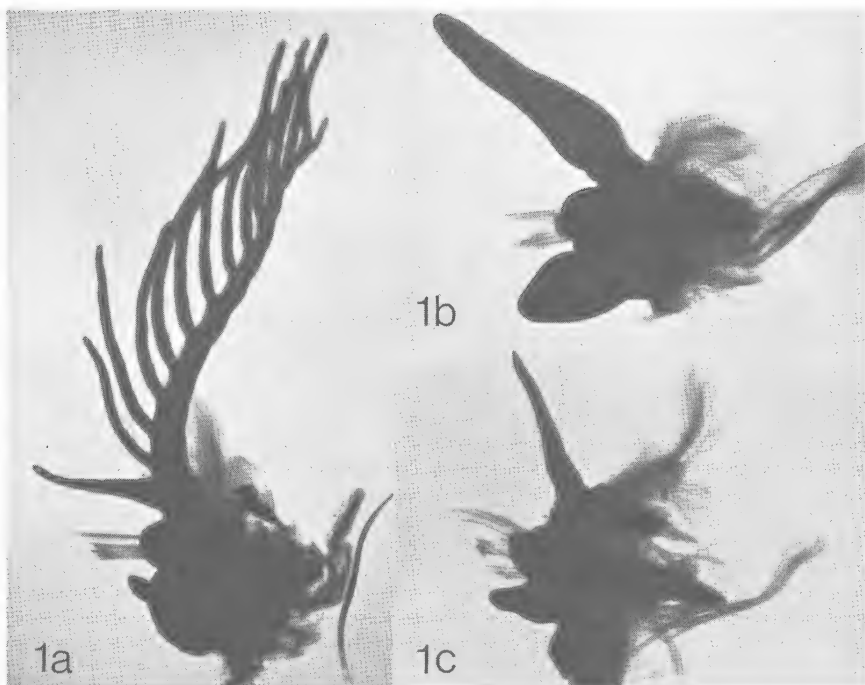


Figure 1. Parapodia from a Turn Point specimen: (a) parapodium with 13 branchial filaments, x12, (b) second parapodium with smooth dorsal cirrus, x23, (c) a posterior parapodium, x23.

Setae of specimens from all collecting areas are quite similar. The only variations noted are that the hood of the subacicular hook is often worn or broken off, and that the serrations on the distal end of the shaft of the compound falcigers are sometimes difficult to resolve.

The setae appear to harbor the most unvarying taxonomic characters, but a comparison of the specimens analyzed here with all six species concerned is precluded since not all types of setae are figured for all species either by the original authors or by Fauchald (1969). The setae of the present material, however, appear similar to those of the *E. kobiensis* holotype and are also similar to those drawn by Fauchald (1969) for both *E. kobiensis* and *E. valens*.

Hartman (1944) has stated that the color patterns of *Eunice* may be taxonomically significant, and Berkeley and Berkeley (1948) use coloration as one key character to separate *E. kobiensis* from *E. biannulata*.

Only the San Juan Island specimens have been observed alive. All of the smallest of these animals had a dark brown "peristomium," pearly white nuchal ring and first setiger, and a mottled brown dorsum just posterior to the nuchal ring (Fig. 3-b). Larger specimens showed an increase in the amount of brown pigment anteriorly with more or less of the white nuchal ring and first setiger mottled with brown (Fig. 3-a). Coloration appears to vary with size (age). The report of *E. biannulata*

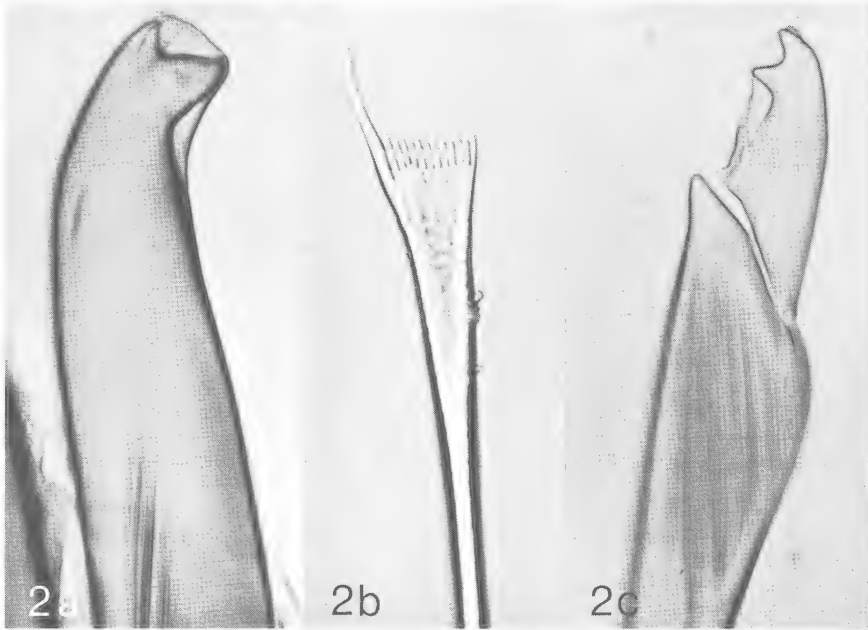


Figure 2. Three types of setae from a Turn Point specimen: (a) a subacicular hook, x620, (b) a comb seta, x900, (c) a compound falciger, x620.

from the British Columbia coast (Berkeley and Berkeley, 1948) is likely erroneous due to reliance on color patterns.

Quantitative Characters

Lengths of live, unbroken, nonregenerating, magnesium chloride-anaesthetized San Juan Archipelago specimens are given in Table 2. Length depends both on age and degree of relaxation of these soft-bodied animals. Mean size of mature specimens may be more taxonomically significant, but not enough data are available.

Setiger counts for all nonregenerating and unbroken specimens are given in Table 2. The taxonomic use of these data is subject to the same criticism as are measurements of total length, except that degree of relaxation of the specimens is here unimportant.

The relative lengths of the tentacles, when given as a proportion of the length of a certain number of anterior setigers, vary with the type of fixation. For example, one of the diagnostic differences between *E. kobiensis* and *E. valens* is that the median tentacle of *E. valens* "barely reaches the second setiger" (Fauchald, 1969), while that of the *E. kobiensis* holotype reaches the eleventh setiger. The holotype of *E. kobiensis* looks as if it had not been relaxed when it was fixed, *i.e.*, all the setigers are very short in comparison to the width. All the present specimens were relaxed before they were fixed, consequently they have relatively long setigers. The median prostomial tentacles reach only as far as the second setiger in the present material. The apparent greater relative length of the *E. kobiensis* holotype median tentacle may be an artifact due to a compression of setigers in the process of fixation. Therefore

TABLE 2. Morphological data. The setiger on which the branchiae cease is given as the maximum value (from left or right side) for specimens 1-58 and 69-90. $\bar{y}$ SJI and $\bar{y}$ Alaska, and 95 percent C.L. SJI and 95 percent C.L. Alaska are the means and 95 percent confidence limits for the San Juan Islands and Aleutian Islands specimens respectively.

Specimen Number	Setiger on Which Branchiae Begin		Setiger on Which Branchiae Cease		Maximum Number of Branchial Filaments	Setiger on Which Branchial Filaments Maximum		Subacicular Hooks Begin		Total Length (mm)	Total Number of Setigers
	Left	Right	Left	Right		Left	Right	Left	Right		
1				75	11	23				250	183
2				78	8	9					
3				71	7	9					164
4				83	10	14					204
5				42	3	9					133
6					3	7					
7				90	10	17					
8				90	7	15					183
9				77	10	13					
10				44	4	8					
11					8	13					
12				81	10	17					
13				68	8	18				180	181
14			108		11	27					
15				58	7	15					
16				51	5	11				85	114
17				88	12	15					
18				61	6	10				150	157
19				80	9	14				155	176
20				78	7	9					166
21				54	6	14				80	126
22				69	6	10					
23				82	9	18					
24					3	7					
25				54	8	13					
26				55	5	11				70	106
27				60	6	12				80	136
28					12	15					
29				91	10	10					207
30				69	9	24					172
31				92	12	18					
32				76	10	13					193
33				76	13	22					200
34				73	9	14					
35				83	14	16					
36				80	13	14				220	206
37				85	11	21				260	201
38				79	8	17					
39				85	8	23				220	187
40				78	11	19					196
41				94	11	26					
42				87	11	15					
43				73	11	25				240	178
44			100		10	12					
45				74	8	12					172
46				85	10	15					
47				93	11	15					
48				70	12	16					
49				93	16	25					
50				74	12	17					
51				84	9	13					
52				86	10	24					211

TABLE 2. (continued)

53			91	13	21				194
54			74	10	18				
55			92	12	22			270	191
56			70	8	8				
57			76	9	14				
58			83	10	17				
59						39	39		175
60						45	42		
61						46	43		
62						38	39		
63						37	34		
64						40	41		
65						44	43		173
66						41	39		178
67						38	40		192
68						47	46		
69			58	6	10				
70			76	7	13				
71			72	9	17				
72			69	11	14				
73			78	11	23			220	179
74			107	10	20				
75			93	13	17			250	169
76			83	9	22				
77			77	9	27				
78			70	11	14				
79			77	8	25			210	194
80			74	12	23			210	168
81			94	15	14				
82			98	11	14			270	197
83			96	9	14			215	179
84			74	6	9				
85			88	11	25				
86			94	11	20				
87			97	9	14			295	195
88			83	11	17			220	180
89			79	12	24				
90			73	9	11			160	179
91	3	3	97	93	12	20	53	50	197
92	3	3	83	77	9	17	36	37	171
93	4	4	51	53	7	15	43	43	
94	5	5	56	59	7	14	52	49	
95	6	6	51	52	6	25	47	47	
96	5	6	50	50	7	25	42	45	118
97	5	4	59	60	8	18	51	50	
98	5	4			8	16	44	46	
99	5	5			8	25	49	49	
100	5	6	50	51	7	19	44	44	
101	4	4	51	49	8	19	40	38	
102	4	5			6	20			
103	5	5			9	26			
104	4	4	46	47	7	19	41	38	
105	3	3	48	49	6	12	36	38	123
106	4	5	45	46	8	27	46	44	
107	4	4	52	52	6	15	46	42	
108	4	5	50	52	6	20	41	38	
109	6	5	50	53	6	28	40	43	
110	5	6	50	51	4	13	37	38	
111	6	5	55	55	7	18	45	45	132
112	4	4	53	54	7	12	37	40	130
113	4	5	49	49	7	13	36	36	
114	5	4	58	58	7	17	44	45	
115	5	4	52	52	6	16	42	40	
116	4	3	54	54	7	15	35	38	126
117	5	3	50	51	7	19	35	35	124
$\bar{y}$ SJI			78		10	16			200
$\bar{y}$ Alaska	5	5	52	52	7	19	42	42	177
95% C.L. SJI			56-100		5-15	7-25			126
95% C.L. Ak.	3-6	3-6	45-58	46-59	5-9	10-27	34-51	35-50	86-314
									136-218
									115-136

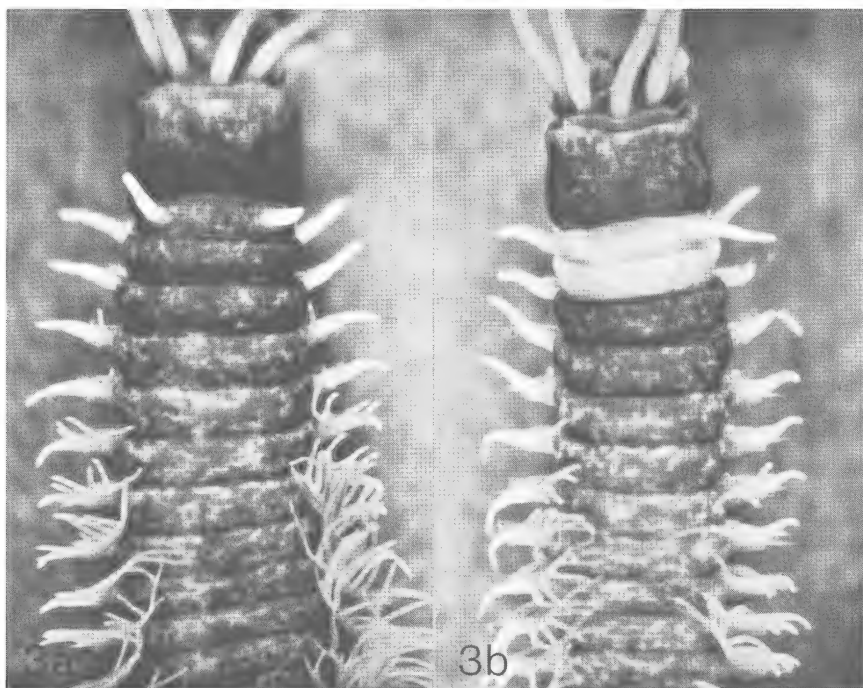


Figure 3. The anterior region of two Turn Point specimens, dorsal view: (a) a larger individual with dark nuchal ring and first setiger, x4, (b) a small individual with white nuchal ring and first setiger, x7.

the present material does not necessarily differ in this character from the holotype of *E. kobiensis*. Furthermore, it is often difficult to judge whether or not the tentacles are distally complete. The tentacles are delicate and evidence of breakage often can be found.

The dentition of ten specimens from Turn Point, San Juan Island, has been analyzed. Teeth counts of maxillary plates are given in Table 3. The general morphology of the maxillae and mandibles is shown in Figure 4. The 95 percent confidence

TABLE 3. Teeth counts for the maxillary plates of ten specimens from Turn Point (#59-#68 of Tables 1 and 2). $\bar{y}$ is the mean value.

Specimen Number	Left Plates			Right Plates	
	II	III	IV	II	III-IV
59	6	7	8	8	9
60	9	8	7	9	16
61	7	8	10	9	10
62	6	7	8	8	10
63	6	7	8	8	10
64	6	8	9	7	10
65	7	8	8	7	13
66	6	8	7	6	12
67	6	8	6	8	9
68	6	8	7	7	9
$\bar{y}$	7	8	8	8	11
95% Confidence Limits	5-8	7-8	6-10	6-9	7-15

limits for these data indicate that there is considerable intrapopulation variation in this character.

In all the San Juan Archipelago specimens (no data given) and the two Victoria specimens the branchiae begin almost invariably on the third setiger. In the Alaskan specimens the branchiae begin anywhere from the third to the sixth setiger, and furthermore this character often differs on the two sides of the same specimen. Hartman (1944) felt that the occurrence of the branchiae is a poor taxonomic character, but Fauchald (1970) disagreed somewhat. He stated that if the first branchia occurs on setiger 3, there is no variation in the first occurrence of the branchiae. The bulk of the San Juan Archipelago and Victoria specimens support Fauchald's statement, but the Alaskan specimens do not. Since the San Juan and Victoria specimens were intertidal and the Alaskan specimens were subtidal to shelf depths, it is possible that this character varies bathymetrically, although Tables 1 and 2 do not support this hypothesis.

The number of the setiger on which the branchiae end, reflecting the number of branchiated setigers when the number of abbranchiated anterior setigers is subtracted from it, was declared highly variable by Hartman (1944). Fauchald (1970) suggested that perhaps the proportion of branchiated to abbranchiated setigers is a constant feature. A plot of the number of branchiated setigers versus the total number of setigers (Fig. 5) shows a weak but real correlation. As the number of segments increase, more segments become branchiated. This character will obviously have very

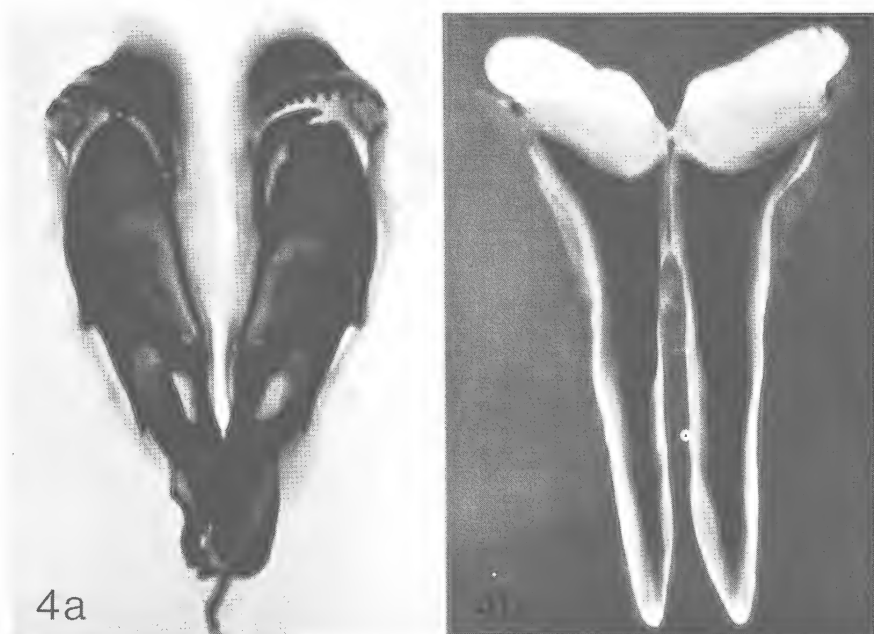


Figure 4. Dental apparatus from two Turn Point specimens: (a) maxillary plates, ventral view, x25, (b) mandibles, ventral view, x25. Note the calcified cutting edges of the mandibles.

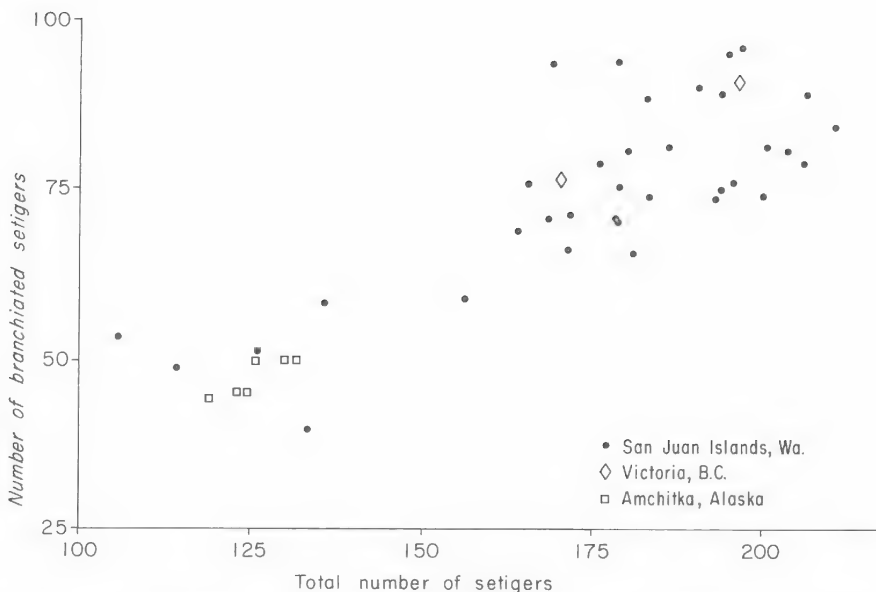


Figure 5. Graph showing the relationship between the number of branchiated setigers and the total number of setigers.

little taxonomic significance unless complete, mature specimens are analyzed. The type specimens of *E. kobiensis*, *E. segregata*, and *E. semisegregata* are all incomplete posteriorly.

The maximum number of branchial filaments varies from three to 16 within a single population (Turn Point specimens). See Figure 1-a for a parapodium with 13 filaments. This character has never before been shown to have this much intra-population variation. A plot of maximum number of branchial filaments versus total number of setigers (Fig. 6) shows a weak positive correlation. Since the total number of setigers probably varies with age, it follows that as the animals get older their branchiae may acquire additional filaments. There is no correlation between maximum number of branchial filaments and bathymetric distribution (note the data for the Amchitka Island specimens, Tables 1 and 2).

In almost all the specimens observed (no data given), the first branchiae were single filaments, but rarely a first branchia had two filaments. When this occurred it did so on one side of the animal only, and therefore is interpreted as a developmental phenomenon.

Subacicular hooks are not present in the anterior region of the body of *Eunice*, and the first setiger on which they are found in the present material shows considerable variation (Table 2). Usually the hooks start further back on one side of the specimen than the other. Furthermore, the hooks might be present on one side, for example, on setigers 36, 37, 38 . . . etc., and on the other side on setigers 36, 38, 39, 40 . . . etc.

A plot of the average setiger number where subacicular hooks begin versus total number of setigers shows no correlation (Fig. 7). This character does not vary

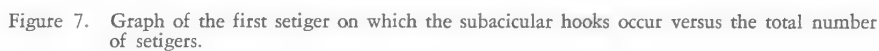
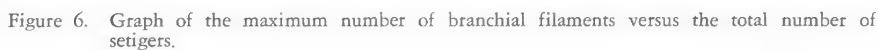


TABLE 4. A comparison of the specimens analyzed in this report with the type specimens of the *Eunice* species known to occur on the northwest coast of North America. An asterisk denotes similarity of character, a blank space denotes a dissimilarity between that species or population and the other species or populations, and a dash indicates a lack of data. The relative reliability of each character is summarized.

[illegible]

with specimen size, and it would make a good taxonomic character were it not for the fact that so much intrapopulation variation is present.

Comb (pectinate) setae of all specimens examined have approximately 12 teeth and one longer lateral fibre (Fig. 2-b). This is similar to *E. kobiensis* but different from *E. segregata* (Fauchald, 1969). The comb setae of the other four species of this group remain undescribed.

Table 4 is a summary of the foregoing data. Most of the characters used to separate these six species have here been shown to have too much intrapopulation variation to be taxonomically useful. The only reliable characters for distinguishing among the species discussed are the form of the parapodial lobes in the branchial region, the number of teeth on the comb setae, the form of the subacicular hooks and compound falcigers, and the structure of the first branchia. *E. valens* is here suggested to be a junior synonym of *E. kobiensis*, since the two are similar in almost all characters here shown to be fairly reliable.

The Amchitka Island specimens have much less morphological variation than do the San Juan Archipelago-Victoria animals, despite their much greater bathymetrical range. This is not likely due to the smaller sample size. In most characters the Amchitka Island specimens resemble the *E. kobiensis* holotype (from Kobé, Japan) more closely than do the San Juan and Victoria animals. It is tempting to hypothesize that a geographical gradient of morphology is present in specimens from various locations in the Aleutian Islands, Alaskan mainland, and British Columbia. However, this would seem inconsistent with the fact that *Eunice* typically has demersal larvae (Akeson, 1967, and author's observations).

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Fluctuations of Aquatic and Terrestrial Invertebrates in Drift Samples from Convict Creek, California

Introduction

Cyclic drift patterns for various aquatic and terrestrial insects in lentic environments should be of primary concern to workers involved in studies of feeding habits and behavioral activities of fishes inhabiting these environments. Waters (1965) divided stream invertebrate drift into three categories: (1) "catastrophic" drift (due to an unusually severe disturbance), (2) "constant" drift (due to an accidental dislodgement), and (3) "behavioral" drift (due to endogenous insect behavior patterns). While most drift organisms appear to be "night" rather than "day" active (Müller, 1966), others appear to be more sensitive to the vicissitudes of stream flow (Anderson and Lehmkuhl, 1968). Many authors (Tanaka, 1960; Waters, 1962; Müller, 1966; Elliott, 1967; and Pearson and Franklin, 1968) have observed a dramatic post-sunset increase in aquatic drift organisms from streams from various geographic regions.

The experimental stream sections at the Sierra Nevada Aquatic Research Laboratory, Bishop, California provide an excellent opportunity for a study of the diurnal drift patterns of aquatic and terrestrial insects in both a riffle and a pool. Also, observations were made of changes of drift abundance and type by artificially altering the water flow and velocity through these areas.

Materials and Methods

The Sierra Nevada Aquatic Research Laboratory, a facility of the Bureau of Sport Fisheries and Wildlife, Division of Fishery Research, is located on Convict Creek on the eastern slope of the Sierra Nevada Mountains in California (lat. 37°37'N, long. 118°50'W) at an elevation of 2195 m (Fig. 1-A). Convict Creek heads from snow-fed lakes encompassing Convict Creek Basin near the precipitous eastern escarpment (average crest elevation 3600 m) and drains an area of 60 km². Convict Creek eventually empties into Crowley Lake (elevation 2070 m), a reservoir for the Los Angeles Department of Water and Power.

Convict Creek is normally very clear, has a rocky substrate derived from glacial outwash material, and is nearly devoid of vascular aquatic vegetation. Although the surrounding terrain to the study area is vegetated with xeric shrubs, the creek is canopied for most of its length with *Populus tremuloides*, *Betula fontinalis*, and *Salix* spp.

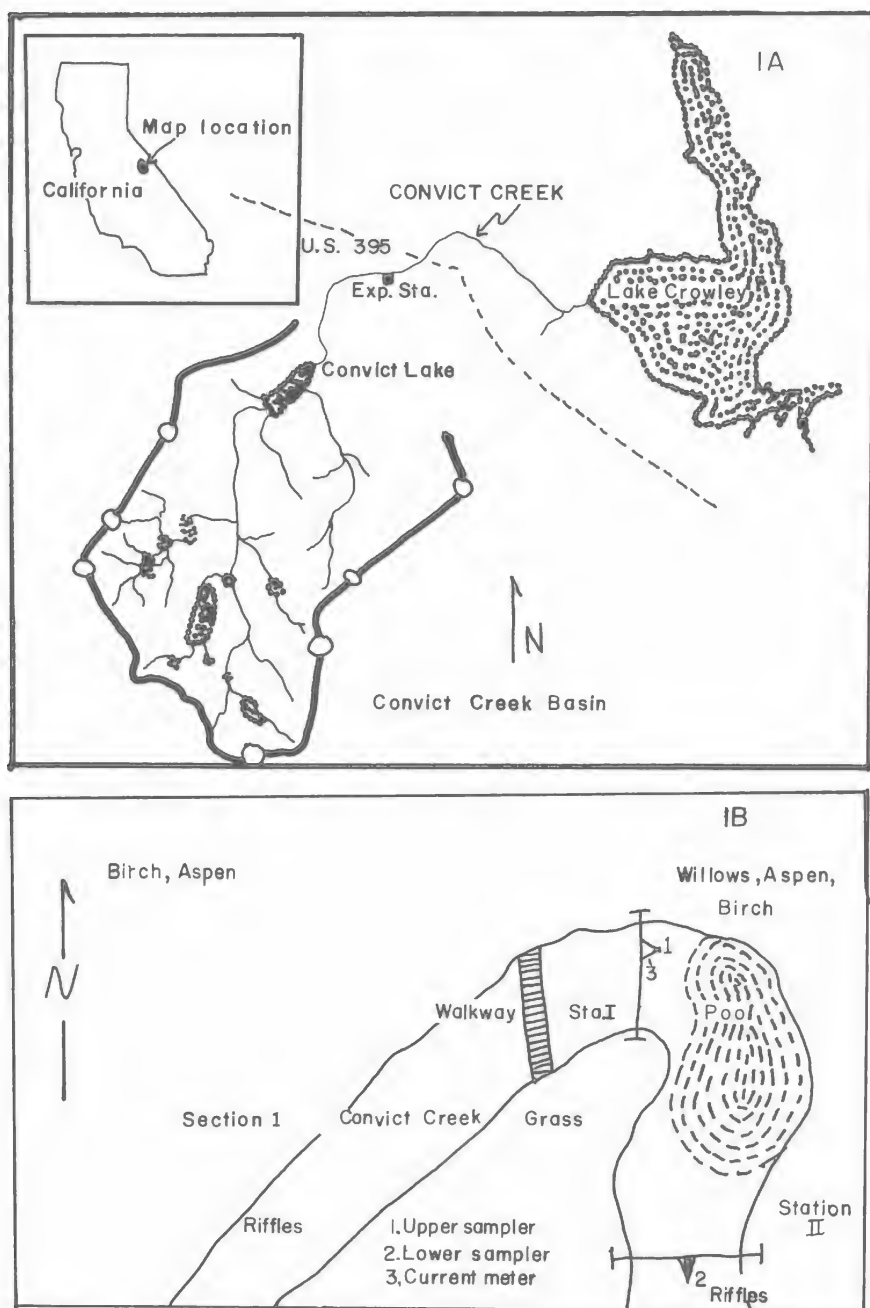


Figure 1. A: Convict Creek watershed and location of U.S. Fish and Wildlife Experiment Station. B: Diagram of sampling locations.

Further description of the lakes in Convict Creek Basin is provided by Reimers *et al.* (1955), and of investigations of Convict Creek by Maciolek and Needham (1951), Reimers (1957), Kennedy (1955 and 1967), and Jenkins (1969).

The main channel of Convict Creek within the grounds of the research area is divided into two 0.8 km sections which are further subdivided in half. An area of study was selected in stream section I and consisted of one riffle-pool complex (Fig. 1-B). The riffle area extends almost continuously upstream for 50 m from sample Station I. Sample Station II was located at the beginning of another riffle area and at the downstream side of a pool. The pool was typical of a more mature stream with a heavily undercut bank and various bars and deeps. The deepest point in the pool was approximately 1.4 m. Sample stations were established by placing sawdust evenly across the entire width of the stream 8 m upstream from the pool and then observing areas of greatest flow. The sawdust entered the pool mainly at the area where Station I was established. The sawdust was well distributed by several turbulent eddies and only a small, rather even proportion emerged at the area where Station II was established.

Aquatic and terrestrial¹-drift organisms were collected in Surber samplers suspended in the area of maximum current velocity. The sampler rested on the substrate so that the sample area was approximately $.07 \pm .01\text{m}^2$. Samples were collected for one hour, placed in 50 percent ethanol solution, and examined within 12 hours of collection. Drift samples were divided into three main classes: organisms of aquatic origin, terrestrial organisms, and egg masses. The aquatic and terrestrial classes were sorted to order or family, recombined, blotted with filter paper for 30 seconds, and weighed to the nearest .001 of a gram. Egg masses were similarly weighed.

Air and water temperatures were continuously monitored at the research station. The water temperature probe was located approximately 50 m upstream from the study area. Current velocity was measured with a Gurley Current Meter three times every hour. The base plate of the current meter was fixed in the stream bed approximately 10 cm from the upstream edge of the Surber sampler at Station I.

Preliminary experiments were conducted at Station I with two Surber samplers located 30 cm apart. Samples were collected from 1000 hours on July 19 until 1700 hours on July 20; from 1700 until 2000 hours on July 27 and August 9; from 0400 until 0900 hours on July 28 and August 10; and from 1100 until 1900 hours on August 12, 1966. The final experiment was conducted with one Surber sampler placed at each Station for a 24-hour period from 1700 hours on August 18 until 1700 hours on August 19.

Results

Results of a preliminary experiment established that a peak in aquatic drift organisms occurred around sunset (Table 1). Mayflies (Ephemeroptera: *Baetidae*: Immatures) were the dominant aquatic organisms while chironomids and crane flies (Diptera: *Chironomidae* and *Tipulidae*: Adults) were the most common terrestrial organisms observed in this postsunset peak. Subsequent experiments were designed to ascertain the causes of this increase in drift activity. Water velocity in this and the other three stream sections could readily be altered by diverting water into or from the

¹Terrestrial insects were defined as those insects which dropped into the stream and became incorporated into the drift material.

TABLE 1. Effect of time on aquatic drift organisms at Station I. Sunset was at 1945 hours.

Date	Time (hours)	Sample weight (grams)	
		Sampler 1	Sampler 2
7-19	1100	.045	.125
7-19	1200	.035	.075
7-19	1600	.020	.045
7-19	1700	.015	.040
7-19	1900	.025	.050
7-19	2000	.165	.235
7-20	0900	.100	.145
7-20	1000	.053	.080
7-20	1600	.032	.045
7-20	1700	.034	.048

other sections. Water velocity was increased by 18 percent at 1800 hours on August 9, and a 32 percent increase in organisms (by weight) was observed from the next sample period (Table 2). However, this increase in stream flow did not appear to cause an increase in bottom-originated organisms, while it did increase terrestrial organisms. These terrestrial organisms included adult forms of black flies (Diptera: *Simuliidae*), chironomids, and crane flies. This qualitative increase in organisms was most likely due to the greater amount of bank vegetation being submerged because of increased stream depth and flow. Subsequent decreases in water velocity did not prevent the observed increase in drift activity at sunset. The mayfly (immatures) was the most dominant aquatic insect found in the 2000- to 2100-hour sample, although chironomids (adults) and crane flies (adults) were the most common terrestrial organisms. There was no correlation between water velocity and weight of organisms ($R^2 = .03$), but a positive correlation did exist between water temperature and weight of organisms ($R^2 = .85$).

The experiment involving changes in water velocity was repeated because of the confounding effect that sunset had on the numbers of organisms present. This next test was conducted during the early afternoon to eliminate this effect. Water velocity was increased 78 percent at 1200 hours on August 12 (Table 3). An immediate in-

TABLE 2. Effect of increasing and decreasing stream flow on drift organisms on August 9. Sunset was at 1935 hours.

Sample Period	Water Temperature (°C)	Water Speed (m/sec)	Organisms (grams)	Number of Organisms		
				Eggs	Aquatic	Terrestrial
1700-1800	20.3 - 20.3	0.45	0.025	0	10	28
1800-1900	20.3 - 20.0	0.53	0.033	0	3	60
1900-2000	20.0 - 19.4	0.50	0.085	0	6	92
2000-2100	19.4 - 19.1	0.47	0.268	57	72	118

TABLE 3. Effect on drift organisms by altering the water velocity. August 12.

Sample Period	Water Velocity (m/sec)	Organisms (grams)	Number of Organisms		
			Eggs	Aquatic	Terrestrial
1100-1200	0.43	0.074	0	10	20
1200-1300	0.76	0.101	0	82	33
1300-1400	0.83	0.088	0	30	31
1400-1500	0.84	0.079	--	----	---
1500-1600	0.81	0.060	--	----	---
1600-1700	0.76	0.048	2	16	17
1700-1800	0.34	0.009	0	5	4

crease in number and weight of organisms was observed, 39 and 282 percent respectively. The greatest proportion of this increase was noted in aquatic chironomids (immatures: from one to 49) and crane flies (immatures: from six to 18), whereas the number of terrestrial organisms only increased from 20 to 33, a 65 percent change which represents an increase proportional to the increase in stream velocity. However, after this initial surge, the numbers and weight of organisms returned to or below pretreatment (1200 hours) levels. By reducing the water velocity at 1700 hours a further decrease in the number of organisms was observed in the sample. In this case, a correlation existed between water velocity and weight of organisms ($R^2 = .41$). A negative correlation was found between water temperature and weight of organisms ($R^2 = .53$). This correlation is opposite to the positive one found for August 9.

The final experiment consisted of a 24-hour sampling period at Stations I and II (Fig. 1-B). Results from these samples were very striking (Fig. 2). There was an explosive increase in the amount of drift organisms approximately one-half hour after sunset (sunset was defined as the time the sun completely disappeared from view behind the Sierra crest) for both sample stations. The majority of drift organisms were aquatic insects although egg masses and terrestrial insects showed some increase at this time. Aquatic insects were the dominant forms through the hours of darkness. At sunrise, there was a sudden drop in the drift of aquatic insects and egg masses.

One sample taken at Station I from 2300 to 2400 hours (Fig. 2) showed a sec-

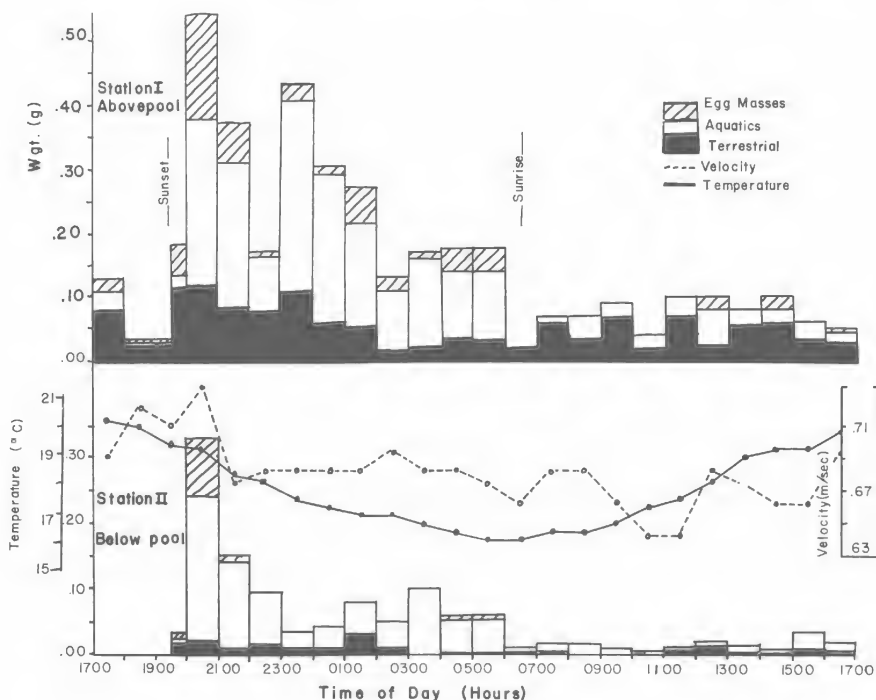


Figure 2. Time course for drift samples from Stations I and II (Fig. 1-B), water temperature, and velocity on August 18 and 19, 1966 at Convict Creek.

ondary increase, mainly in aquatic insects, which could have been caused by the disappearance of the moon (2245 hours), consequently, an almost total reduction in light. The sample at Station II did not respond to this change in light. The constant and relatively low level for all three classes from samples at Station II might have been caused by (1) the low and even discharge across the base of the pool, (2) the turbulent mixing action of the pool and the settling out of some organisms, (3) removal of organisms at Station I, and (4) by fish which inhabited the pool. This pool contained a mixed population of brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*). These fish were observed to be feeding during the night at a position in the pool where the sawdust had been observed to roll and tumble.

Throughout the daylight hours, the drift of terrestrial and aquatic insects remained at a low level while egg masses were collected in only a few samples. There was a decrease of chironomids (adults) in the samples after 2100 hours and a corresponding increase of the mayfly (immatures). At sunrise, the presence of mayflies was considerably less than during the night. Caddisflies (Trichoptera: *Rhyacophilidae* and *Limnophilidae*: immatures) and beetles (Coleoptera: *Elmidae*: immatures) were also more prevalent during conditions of darkness.

Over the 24-hour period, a total of 1755 organisms was counted from the three classes for all samples taken at Station I, and only 912 organisms from Station II. For all 48 samples, aquatic insects comprised 68.1 percent of the total collected, terrestrial insects 25.0, and egg masses 6.9.

Discussion and Conclusions

Aquatic and terrestrial organisms appeared to be principally "night" active in Convict Creek. Jenkins (1969) observed a similar pattern from another section of Convict Creek on August 12 and 13, 1966. Aquatic mayflies and both aquatic and terrestrial chironomids and crane flies were the organisms that showed the greatest response during the period of sunset. Similar results were noted by Pearson and Franklin (1968) and by Anderson and Lehmkuhl (1968).

Reduction in light intensity (Tables 1, 2 and Fig. 2) had a dramatic effect on both the numbers and weight of organisms sampled. Possibly the activity of aquatic organisms was even sensitive to changes in moonlight (2300 to 2400 hour sample, Fig. 2). Hughes (1966) and Elliott (1967) maintain that the absence of light causes disorientation of many aquatic organisms, hence their potential to drift, and therefore a passive rather than an active response. In contrast, Holt and Waters (1967) demonstrated a negative photoactive response in certain "night" active organisms.

An increase in water velocity in the stream section increased the terrestrial drift. This appeared to be proportional to the increased flow through the sampler (Tables 2 and 3). However, an extreme increase in stream flow resulted in an appreciable increase in aquatic insects (Table 3). The number of these aquatic insects decreased rapidly in the second hour following this increase in water velocity (1300 to 1400 hours: Table 3), while the number of terrestrial insects remained constant. This type of drift pattern probably is included in Waters' (1965) definition of "catastrophic" drift. In the absence of abnormal fluctuations in water velocity, the weight of drift organisms was not correlated with diurnal changes in stream velocity caused by repeated thawing and freezing of upper elevation snow. Similarly, water temperature did not appear

to influence drift except perhaps between 1700 and 2100 hours (Table 2). This is evidently a correlative rather than a causative relationship. The absence or presence of light was the dominant factor controlling the magnitude of aquatic drift organisms.

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Comparative Food Habits of Four Species of Stream-Dwelling Vertebrates (*Dicamptodon ensatus*, *D. copei*, *Cottus tenuis*, *Salmo gairdneri*)

When two or more species occupy the same habitat and have the same requirements for food and space, supposedly limited in supply, then these species are in direct competition. Ultimately, the least adapted species may be excluded from the competitive arena. This is a simplification of Gause's Principle (1934) or Hardin's "competitive exclusion principle" which states that complete competitors cannot occupy the same niche (Smith, 1966). If the niches (niche is defined here as the residential and nutritional requirements of an organism) only partially overlap, then the organisms involved may coexist, and often behavior mechanisms serve to establish partial exclusion. For example, MacArthur (1958) found that several species of warblers with similar food habits were able to coexist in the same wood by a combination of adaptations including partitioning of the forest canopy and selective feeding by at least one species.

Four species of cold-blooded vertebrates often occur together in northwestern streams. These are: *Dicamptodon ensatus* (Pacific giant salamander), *Dicamptodon copei* (Cope's salamander), *Cottus tenuis* (slender sculpin), and *Salmo gairdneri* (rainbow trout). Only the branchiate, larval forms of the two salamanders are of interest in this study.

Casual observations suggested that the habitats of these four species were similar, especially among smaller individuals. Individuals of all species take cover under rocks and logs and in crevices, and often individuals of two or more of the species can be found sharing the same hiding place. In light of these observations, it was thought that a comparative study of the food habits of these four species within a single section of a stream would help to reveal the role that each of the species has in the stream community, and that possible exclusion mechanisms might be found.

The food of *S. gairdneri* is generally known through a widely scattered literature. Bailey's (1952) study of the food of *Cottus bairdi* suggests that freshwater cottids are largely opportunistic feeders, although he gave no information on availability.

Dineen (1951) studied the comparative food habits of *C. bairdi* and sympatric species of trout. His study included information on food availability and stomach contents and indicated that major food items were similar but that competition may be relaxed by differential feeding behavior at certain times of the year. Dineen also noted that cottids are mainly bottom feeders whereas salmonids feed at all levels.

Metter (1963) studied the food of larval *D. ensatus* in a small stream in Latah County, Idaho. He found that 52 percent of the stomachs contained trichopteran larvae and 14 percent tadpoles of the tailed frog, *Ascaphus truei*. Both of these items were abundant in the stream studied. Johnson and Schreck (1969) examined the stomach contents of 51 larval *D. ensatus* from Fern Lake, Humboldt County, California. They found that 70.5 percent of the larvae had eaten Odonata nymphs, and that 39.2 percent had eaten larvae of the northwestern salamander, *Ambystoma gracile*. Odonata nymphs and larvae of *A. gracile* are known to be common in ponds and lakes and rare or absent in streams. Warren *et al.* (1969) examined stomachs of *D. ensatus* larvae from Berry Creek, Benton County, Oregon. The snail, *Oxytrema* sp., was the most common food item and parts of crayfish were found in several stomachs. *Oxytrema* is exceedingly abundant and crayfish common in Berry Creek. Franz (1970) reported that larval *D. ensatus* regurgitated caddisfly cases of a species common in the small pond from which the larvae were collected. These and numerous other observations (Nussbaum, unpubl.) indicate that larval *D. ensatus* can easily adapt to different kinds of food in different environments and that, in general, they feed on whatever is most abundant.

The purpose of this study was to determine which aspects of "partial exclusion" might be responsible for the coexistence of the four species in a mountain stream in southwestern Washington.

At the time of this study only one species of *Dicamptodon* (*D. ensatus*) was known, and therefore only one salamander was considered in the analysis. Nussbaum (1970), since then, has determined that the *Dicamptodon* complex contains two species, *D. copei* and *D. ensatus*, and that the two occur at the study site. Therefore, all gut analyses are for *D. ensatus* and *D. copei*, collectively, and any reference to food items shall refer to *Dicamptodon* spp.

Methods and Materials

The Study Site

A 500-ft section of Maratta Creek was chosen as the study site. Maratta Creek is a tributary of the Toutle River located on the western slopes of the Cascade Mountains in Cowlitz County, Washington (T9N, R4E, Sec. 3). The stream is about 1.5 mi long, heading at 2740 ft and ending at 2100 ft with an 8 percent gradient. Vegetation at the study site is largely old growth Douglas-fir with some western red cedar. Undergrowth is sparse. Precipitation is about 80 in per year. The stream is clear and rocky-bottomed with abundant cover provided by fallen logs. Discharge during the 12-month study period (April, 1968 to March, 1969) varied from 6 cfs in July to 188 cfs in March. Stream temperatures ranged from 1°C in April, December, and February to 15°C in July. Diel temperature fluctuations ranged from 0.5°C in April and December to 5°C in October. Dissolved oxygen varied from 9.9 ppm in July to 12.7 ppm in February. The range of pH was 7.0 to 7.3, with the low readings in the summer months and the high readings in the winter months.

Sampling Methods

Ten random samples, five in mid-stream and five near the sides, were taken each month with a square-foot Surber bottom sampler within the 500-ft study section. The sample sites were selected using a random numbers table system. Samples were placed in jars containing 70 percent alcohol and taken back to the lab where bottom organisms were separated from the rubble and debris. The organisms were then sorted according to order and identified to family. All individuals were labeled and preserved, and are housed at Central Washington State College. Salamanders and fish were normally collected at night, although some were collected during daylight hours. Sample sizes are listed in Table 1.

TABLE 1. Numbers of stream-dwelling vertebrates taken at study site.

Name	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Feb.	Mar.
<i>Dicamptodon</i> spp.	19	20	27	34	9	19	3	0	0	1	0
<i>Cottus</i> <i>tenuis</i>	12	5	9	20	3	6	5	2	0	0	1
<i>Salmo</i> <i>gairdneri</i>	14	17	14	9	27	22	27	15	1	6	8

Three techniques were used to collect vertebrates. A standard fish shocker was employed at the beginning of the project. A seine net gave good results in trapping trout and was generally employed for catching these animals. Salamanders and sculpins could not be caught in this manner and the best method used for trapping them can best be described as a "chase and corral" technique whereby an individual was forced by hand into a dipnet.

As soon as possible after animals were captured they were anesthetized. Two percent chlorotone was adequate for immobilizing the salamanders, after which they were injected with 2-3 cc of 10 percent formalin, put in formalin for several hours, and then preserved in 70 percent alcohol. The fish were put directly into 10 percent formalin. However, they were placed in separate containers because formalin often caused regurgitation of stomach contents and care had to be taken to prevent mixing of stomach contents in a common container. The stomachs were removed and preserved in labeled vials containing 70 percent alcohol.

Results and Discussion

Bottom Fauna

Bottom sample data are summarized in Table 2. The frequency and density of each type of bottom organism are listed by month from April, 1968 to March, 1969. Frequency is the percent of samples in which a particular type of organism occurred, and density is the mean number of individuals per sample.

Food items were categorized as sparse ($.00 > \text{freq.} < .10$), moderately abundant ($.10 \geq \text{freq.} \leq .40$), and abundant ($.40 > \text{freq.} \leq 1.00$). Those families in the abundant category are referred to as "stream staples."

Mayflies, caddisflies, stoneflies, two families of dipterans, one family of beetles, and a small white oligochaete comprise the most abundant food organisms in the stream. In general this was true for the duration of the study. Of the mayflies, baetids, heptageniids, and ephemereleids were abundant. Siphonurids and leptophlebiids

TABLE 2. Average frequency/density of stream organisms taken in bottom samples.

Food Item	Apr.	May	June	July	Sept.	Oct.	Nov.	Dec.	Feb.	Mar.
<i>INSECTS</i>										
<i>EPHEMEROPTERA</i>										
Siphonuridae	30/ 0.5	20/ 1.2	70/ 6.1	70/ 3.8	----	10/ 0.1	----	----	20/ 0.6	30/ 1.3
Baetidae	70/18.8	70/10.0	70/ 4.6	70/ 6.2	60/ 3.7	40/ 0.7	80/ 3.1	50/ 2.3	40/ 4.4	60/ 2.8
Ephemerellidae	70/ 2.7	80/ 2.4	70/ 4.7	60/ 2.7	40/ 5.1	70/ 3.7	80/ 4.6	70/10.3	40/ 7.8	50/ 2.9
Heptageniidae	60/ 8.6	70/ 8.7	60/ 4.8	70/ 1.6	70/ 1.6	70/14.3	60/14.6	80/18.3	40/19.9	50/11.8
Leptophlebiidae	20/ 0.3	40/ 1.5	40/ 2.0	50/ 3.2	---	30/ 0.3	10/ 0.1	10/ 0.6	40/ 0.9	30/ 2.6
<i>PLECOPTERA</i>										
Perlodidae	10/ 0.1	30/ 0.6	50/ 1.1	70/ 1.4	70/ 2.1	30/ 0.4	70/ 1.2	50/ 1.2	40/ 0.5	40/ 1.1
Chloroperlidae	10/ 0.4	60/ 1.5	50/ 1.0	20/ 0.4	30/ 0.6	40/ 0.9	50/ 2.5	60/ 1.6	30/ 1.4	40/ 1.8
Perlidae	20/ 0.2	10/ 0.1	10/ 0.1	60/ 0.2	70/ 2.4	60/ 2.0	50/ 1.9	60/ 2.2	30/ 0.5	20/ 0.3
Nemouridae	60/ 1.8	----	20/ 0.5	----	----	30/ 0.4	----	60/ 4.4	40/34.3	40/ 5.6
Peltoperlidae	----	---	----	10/ 0.1	----	----	----	----	----	----
<i>TRICHOPTERA</i>										
Rhyacophilidae	----	10/ 0.2	30/ 0.6	40/ 0.6	---	40/ 0.5	----	50/ 0.6	30/ 0.9	10/ 0.1
Limnephilidae	---	---	10/ 0.1	90/ 6.6	40/ 1.7	50/ 2.7	10/ 0.2	10/ 0.1	20/ 0.4	40/ 1.5
Lepidostomidae	40/ 0.5	40/ 2.9	30/ 1.2	70/ 3.8	50/ 1.4	70/ 1.2	30/ 1.3	40/ 1.0	20/ 0.5	50/ 1.4
Hydropsychidae	50/ 0.6	40/ 0.5	----	20/ 0.2	40/ 6.7	60/ 6.9	50/ 1.0	60/ 2.3	30/ 1.0	30/ 3.0
Glossomatidae	10/ 0.1	40/ 0.4	20/ 0.3	50/ 0.7	50/ 5.7	70/15.7	80/ 2.6	80/ 5.8	30/ 0.8	30/ 1.0
Philopotamidae	----	---	----	20/ 0.3	----	----	----	----	----	----
Psychomyiidae	10/ 0.1	10/ 0.1	---	---	----	----	----	----	----	----
Brachycentridae	----	10/ 0.1	----	----	10/ 0.6	----	10/ 0.1	---	----	----
<i>DIPTERA</i>										
Chironomidae	----	10/ 0.1	30/ 0.5	60/ 1.6	----	----	----	20/ 0.6	40/ 0.6	20/ 0.2
Tipulidae	20/ 0.2	40/ 1.0	60/ 1.3	90/ 7.1	50/ 1.5	70/ 1.4	40/ 0.6	30/ 0.6	30/ 2.3	10/ 0.2
Simuliidae	----	----	10/ 0.2	10/ 0.1	----	10/ 0.1	40/ 1.6	50/10.9	40/ 0.6	20/ 0.3
Blepharoceridae	10/ 0.1	10/ 0.3	----	----	---	----	----	----	----	----
Sciariidae	----	----	----	----	----	10/ 0.1	----	----	----	----
Rhagionidae	----	---	---	20/ 0.2	10/ 0.1	20/ 0.2	---	---	---	---
<i>COLEOPTERA</i>										
Elmidae	30/ 0.4	10/ 0.5	40/ 0.8	70/ 5.6	70/12.2	70/10.1	60/ 1.2	50/ 0.9	40/ 7.0	10/ 0.1
Haliplidae	10/ 0.2	----	----	----	----	----	----	----	----	----
Dytiscidae	----	----	----	10/ 0.1	----	----	----	----	----	----
Ptilodactylidae	----	----	----	----	----	----	20/ 0.2	---	---	---

TABLE 2 (Continued)

Food Item	Apr.	May	June	July	Sept.	Oct.	Nov.	Dec.	Feb.	Mar.
<i>INSECTS</i>										
<i>COLLEMBOLA</i>										
Sminthuridae	---	---	10/ 0.1	---	---	---	---	---	---	---
Entomobryidae	---	---	---	10/ 0.1	---	---	---	---	---	10/ 0.1
<i>OTHER</i>										
Oligochaetes	20/ 0.2	20/ 0.7	20/ 0.8	60/ 3.6	40/ 6.2	70/24.9	80/26.9	90/17.3	40/ 3.8	40/ 4.7
Nematomorpha	---	10/ 0.1	20/ 0.2	20/ 0.3	10/ 0.1	---	---	---	---	---
Nematodes	---	---	---	---	10/ 0.1	---	10/ 0.1	---	---	---
Turbellarians	30/ 0.5	---	---	30/ 0.8	10/ 0.3	20/ 0.3	20/ 0.2	---	---	---
Spider	---	---	10/ 0.1	---	---	---	---	---	---	---
Eggs	---	---	20/ 0.2	20/ 0.2	---	---	---	10/ 0.1	10/ 0.1	---
<i>A. truei</i>	---	10/ 0.1	---	---	---	---	---	10/ 0.1	---	---
<i>S. gairdneri</i>	---	---	20/ 0.3	---	---	---	---	---	---	10/ 0.1
<i>C. tenuis</i>	---	---	20/ 0.3	---	---	---	---	---	---	---

were abundant to moderately abundant depending upon the time of year. Of the caddisflies, limnephileids, lepidostomids, and glossosomatids were abundant with a few exceptions. The other families of trichopterans were sparse to moderately abundant with a few cases of abundant, depending upon time of year. The stoneflies listed were abundant to moderately abundant with Perlodidae being the most common family. One exception was evident in the family Peltoperlidae. This group occurred only once in July, 1968 with one representative individual. Chironomidae and Tipulidae were the most commonly occurring families of Diptera. Tipulids were moderately abundant to abundant. Chironomids were never more than moderately abundant and not taken at all in some months. Elmidae was the only family of coleopterans that occurred significantly in the samples. They were abundant during the summer months and sparse at the beginning and end of the study. Except at the beginning of the study, oligochaetes were always at least moderately abundant. Many other families occurred in the samples but in general they were sparse or infrequent.

Gut Analyses

Records for gut analyses can be found in Tables 3-5. In general, the common stream organisms, with the exception of oligochaetes, were eaten in proportion to their availability. The sculpins appear to be an exception to this in that they seem to prefer siphonurids, limnephilids, and chironomids. Chironomids occurred in the stomachs of sculpins at all times, but did not appear in bottom samples in April, September, October, or November of 1968. Siphonurids did not occur in bottom samples during September, November, or December of 1968 but were found in sculpins in September and November. Siphonurids were in limited numbers in the stomachs of *Dicamptodon* spp. and *S. gairdneri* in September but not when they did not occur in stream samples during November and December. Chironomids were frequent in both *Salmo* and *Dicamptodon* spp., even in months when they were not found in stream samples. The other staples occurred in sculpins, but in extremely low numbers relative to the three families already mentioned. Many of the families found in *Salmo* and *Dicamptodon* did not occur in sculpins. Two sculpins were collected which had eaten small trout. Nematodes were nearly always found in *Cottus* but these organisms may well be parasites.

Dicamptodon spp. appeared to be extremely opportunistic, feeding on what was available at the time. The stream staples comprised the bulk of their diet. Emergent adults and allochthonous or foreign organisms added variety to their diets, but were sparse relative to their major food items. Young salmonids and sculpins frequent their diets during summer low water periods when the concentration of fish is greatest.

Salmo, as in the case of *Dicamptodon* spp., appears to be extremely opportunistic and feeds on all the staples of the stream. But in addition to the stream staples, a great variety of nonaquatic families and emergent aquatic adults were also eaten. This was true throughout the year, but especially so during the months of maximum emergence and activity over the stream. Adult tipulids, adult nemourids, leafhoppers, tree hoppers, spiders, centipedes, and a variety of terrestrial beetles are some examples of these allochthonous types. These items occur rarely in *Dicamptodon* spp. and scarcely at all in *Cottus* (Fig. 1). Dineen (1951) did not indicate this difference of autochthonous and allochthonous material in his comparison of trout and sculpin diets.

TABLE 3. Average frequency/density of food organisms found in *Dicamptodon* spp. by month¹

Food Item	Apr.	May	June	July	Aug.	Sept.	Oct.
<i>INSECTS</i>							
<i>EPHEMEROPTERA</i>							
Siphonuridae	40/ 1.0	55/ 1.6	18/ 0.4	35/ 0.8	22/ 0.6	16/0.16	30/ 0.6
Baetidae	11/0.11	35/0.35	11/0.11	56/ 2.3	33/ 0.6	---	---
Ephemerellidae	31/ 0.5	25/ 0.6	15/ 0.5	44/ 1.0	22/ 1.0	10/ 0.1	---
Heptageniidae	21/ 0.6	55/ 1.3	11/ 0.3	24/ 0.6	22/ 0.2	10/ 0.1	30/ 0.3
Leptophlebiidae	25/ 0.5	55/ 1.7	26/ 3.3	29/ 1.1	11/0.11	53/ 1.8	30/ 0.3
<i>PLECOPTERA</i>							
Perlodidae	11/0.11	10/ 0.1	---	29/ 0.4	---	21/ 0.2	---
Chloroperlidae	25/ 0.3	30/ 0.7	4/0.03	18/0.21	---	10/ 0.1	---
Perlidae	---	---	---	6/0.06	---	---	---
Nemouridae	25/ 0.5	---	---	23/ 0.3	22/ 0.2	---	---
<i>TRICHOPTERA</i>							
Rhyacophilidae	5/0.05	10/ 0.4	---	12/ 0.2	---	10/ 0.1	---
Limnephilidae	---	5/0.05	4/0.03	44/ 1.6	66/ 1.6	32/ 0.5	---
Lepidostomidae	5/0.05	5/ 0.1	---	6/ 0.2	22/ 0.5	21/ 0.2	---
Hydropsychidae	5/0.05	---	---	6/0.06	---	---	---
Glossosomatidae	---	---	---	6/0.09	---	---	---
Philopotamidae	---	---	---	6/0.12	---	---	---
<i>DIPTERA</i>							
Chironomidae	21/ 0.2	25/ 0.4	19/0.22	38/ 0.6	22/ 0.3	26/ 0.3	---
Tipulidae	---	25/ 0.4	11/0.19	8/0.08	22/ 0.2	10/ 0.2	---
Tabanidae	---	---	---	---	11/ 0.1	---	---
Simuliidae	---	5/0.05	---	18/0.24	---	---	---
<i>COLEOPTERA</i>							
Carabidae*	---	10/ 0.2	---	3/0.03	11/ 0.1	---	---
Cerambycidae*	---	---	---	---	---	5/0.05	---
Elmidae*	---	---	4/0.03	12/ 0.1	22/ 0.2	10/ 0.2	---
Elmidae	---	---	4/0.03	3/0.03	---	---	---
Dytiscidae*	5/0.05	---	---	---	---	5/0.05	---
<i>HOMOPTERA</i>							
Membracidae*	---	---	---	---	11/ 0.1	---	---
Cercopidae*	---	---	---	---	11/ 0.1	---	---
<i>HYMENOPTERA</i>							
Tenthredinidae*	---	---	---	---	11/ 0.1	5/0.05	---
<i>LEPIDOPTERA</i>							
Orthoptera	---	---	37/0.04	3/0.03	---	---	---
<i>ORTHOPTERA</i>							
Gryllidae*	---	---	---	---	11/ 0.1	---	---

TABLE 3 (Continued)

<i>OTHER</i>							
Pelycepoda	----	15/0.15	----	----	----	----	----
Gastropoda	---	5/0.05	----	3/0.12	----	----	----
Spider*	---	5/0.05	----	----	----	5/0.05	----
Mite	5/0.05	---	----	----	----	----	----
Nematode	----	----	----	3/0.03	----	----	----
Detritus	16/ 0.3	5/0.15	11/0.11	12/ 0.2	11/ 0.1	21/ 0.2	----
<i>Salmo</i>	5/0.05	---	11/0.33	9/ 0.2	11/ 0.1	5/0.05	----
<i>Cottus</i>	---	---	4/0.03	3/0.03	----	----	----

¹ No organisms were found in stomachs from November to March. *Adult.

TABLE 4. Average frequency/density of food organisms found in *Cottus tenuis* by month.¹

Food Item	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Mar.
<i>INSECT</i>									
<i>EPHEMEROPTERA</i>									
Siphonuridae	42/ 0.7	20/ 0.2	22/ 0.2	50/ 1.0	66/ 0.6	33/ 0.5	20/ 0.2	50/ 0.5	.
Baetidae	50/ 0.6	40/ 0.6	----	15/0.35	---	17/ 0.2	----	----	---
Ephemerellidae	50/ 1.3	40/ 0.6	----	20/0.25	----	----	----	----	----
Heptageniidae	17/ 0.3	----	----	5/0.05	----	17/ 0.2	20/ 0.2	----	----
Leptophlebiidae	----	40/ 1.4	----	20/ 0.2	----	17/ 0.2	----	----	---
<i>PLECOPTERA</i>									
Perlodidae	17/0.17	----	----	20/ 0.4	----	----	---	----	----
Nemouridae	17/ 0.3	----	----	5/0.05	----	17/ 0.2	----	50/ 0.5	----
Chloroperlidae	17/ 0.3	----	----	----	----	----	---	50/ 0.5	.
<i>TRICHOPTERA</i>									
Rhyacophilidae	----	20/ 0.2	11/ 0.1	5/0.05	----	----	----	.	----
Limnephilidae	----	----	22/ 0.2	40/ 1.2	33/ 0.3	33/ 0.3	60/ 3.2	----	----
Lepidostomidae	8/0.25	20/ 0.2	----	----	----	----	----	----	----
Hydropsychidae	8/0.08	----	----	----	----	----	----	50/ 0.5	----
Glossosomatidae	----	----	----	----	----	----	40/ 0.4	----	----
<i>DIPTERA</i>									
Chironomidae	42/ 1.6	60/ 0.6	56/ 1.7	50/ 1.2	66/ 0.6	83/ 7.8	20/ 0.6	50/ 0.5	100/ 2.0
Tipulidae	----	----	----	5/0.05	----	----	20/ 0.2	50/ 0.5	100/ 1.0
<i>COLEOPTERA</i>									
Elmidae*	----	----	----	----	33/ 1.3	----	----	---	----
Elmidae	----	----	----	20/ 0.3	----	----	40/ 0.4	---	100/ 1.0
Dytiscidae*	----	----	----	5/0.05	----	----	----	----	----
<i>OTHER</i>									
Pelycepoda	8/0.8	40/ 0.4	----	----	----	----	---	50/ 0.5	----
Mites	----	----	----	5/0.05	33/ 0.3	---	----	----	----
Nematode	42/ 0.8	20/ 0.4	22/ 0.3	5/0.05	33/ 0.3	----	20/ 0.2	----	----
Detritus	8/0.08	20/ 0.2	11/ 0.1	5/0.05	----	----	----	----	----
Salmo	----	----	11/ 0.2	----	33/ 0.3	----	----	----	---

¹ No organisms were found in stomachs during December and February. *Adult.

TABLE 5. Average frequency/density of food organisms found in *Salmo gairdneri* by month.¹

Food Item	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Feb.	Mar.
<i>INSECTA</i>										
<i>EPHEMEROPTERA</i>										
Siphonuridae	7/0.07	12/0.12	21/ 0.2	66/ 1.0	11/0.15	14/0.18	---	---	17/0.17	13/0.25
Baetidae	7/0.07	18/0.18	36/ 0.6	100/ 8.8	22/ 0.4	14/0.36	---	13/0.13	---	13/0.13
Ephemerellidae	---	12/0.12	14/0.14	33/ 0.6	---	14/0.18	---	---	---	38/ 0.4
Heptageniidae	7/0.07	12/0.12	14/ 0.2	22/ 0.6	4/0.04	9/0.09	3/0.07	7/0.07	---	13/0.25
Leptophlebiidae	---	---	---	22/ 0.6	7/0.07	14/0.18	---	---	---	13/0.13
<i>PLECOPTERA</i>										
Perlidae	---	---	14/0.14	45/ 1.3	11/0.15	5/0.05	7/0.07	---	---	---
Peltoperlidae	---	---	---	---	---	---	---	---	---	13/0.13
Chloroperlidae	---	12/0.18	---	22/ 0.2	7/0.07	9/0.09	3/0.03	---	17/0.17	---
Perlidae	---	---	---	---	---	---	---	7/0.07	---	---
Nemouridae	7/0.07	24/0.35	---	56/ 0.9	11/ 0.1	---	---	7/0.13	---	25/ 0.4
Nemouridae*	---	---	---	---	---	14/0.14	3/0.03	---	---	38/ 0.5
Rhyacophilidae	7/0.07	---	---	11/0.45	7/ 0.1	14/0.14	11/ 0.1	7/0.07	---	---
Limnephilidae	14/0.14	12/0.12	---	---	4/0.04	27/ 0.3	3/0.03	---	---	---
Lepidostomidae	---	---	14/ 0.9	33/ 0.3	11/0.11	9/0.27	7/0.07	7/0.07	17/0.17	---
Hydropsychidae	---	---	---	---	4/0.07	14/0.14	7/0.15	7/0.07	---	---
Glossosomatidae	---	---	---	---	11/0.15	5/0.05	3/0.03	7/0.07	---	---
Trichoptera*	---	---	14/ 0.3	---	15/0.15	---	---	---	---	13/0.13
<i>DIPTERA</i>										
Chironomidae	14/ 0.4	41/ 2.5	71/ 4.9	100/13.0	90/ 7.0	68/ 2.6	22/ 0.2	20/ 0.2	50/ 0.8	50/ 3.1
Tipulidae	---	---	---	22/ 0.2	11/ 0.1	9/0.18	11/ 0.1	---	---	---
Tipulidae*	36/ 1.1	59/ 1.4	43/0.86	33/ 0.6	15/0.15	32/ 0.6	48/ 1.2	7/0.07	66/ 0.8	63/ 2.1
Ceratopogonidae	---	---	---	---	---	9/0.09	---	7/0.07	---	13/0.13
Simuliidae	---	12/0.12	14/0.14	33/ 0.6	22/ 0.5	14/0.14	---	---	17/0.17	---
Simuliidae*	---	---	14/0.14	---	---	---	11/0.18	---	---	38/ 0.4
<i>COLEOPTERA</i>										
Scolytidae*	---	---	---	---	4/0.04	---	---	---	---	---
Staphylinidae*	---	---	---	11/ 0.1	7/ 0.2	---	---	---	---	---
Lagriidae*	---	---	7/0.07	---	---	---	---	---	---	---
Mordellidae*	---	---	---	---	4/0.04	---	---	---	---	---
Carabidae*	---	---	---	---	---	---	3/0.03	---	---	---
Hydrophilidae*	---	---	---	---	---	---	3/0.03	---	---	---

TABLE 5. (Continued).

Food Item	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Feb.	Mar.
<i>INSECTS</i>										
<i>COLEOPTERA</i> (cont.)										
Scarabaeidae*	---	---	---	---	7/0.07	---	3/0.03	---	---	---
Elmidae*	---	---	21/ 0.2	11/ 0.1	7/0.07	9/0.09	15/0.15	7/0.07	---	---
Elmidae	---	---	---	11/ 0.1	---	5/0.05	15/ 0.9	---	---	---
Pselaphidae*	---	6/0.06	14/0.14	---	7/0.07	---	3/0.03	---	---	13/0.13
Dytiscidae*	---	---	---	---	---	---	3/0.03	---	17/0.17	---
Chrysomelidae*	---	---	---	---	11/0.18	5/0.05	7/0.07	---	---	---
Tenebrionidae*	---	---	---	---	7/ 0.1	---	---	---	---	---
<i>HOMOPTERA</i>										
Cicadellidae*	---	18/ 0.2	---	11/ 0.1	33/ 0.2	5/0.05	---	7/0.07	---	---
Membracidae*	---	---	---	---	15/ 0.2	---	3/0.03	---	---	---
<i>HEMIPTERA</i>										
Gerridae*	---	---	---	---	4/0.04	---	---	---	---	---
Scutelleridae*	---	---	7/0.07	---	4/0.04	---	---	---	---	---
<i>HYMENOPTERA</i>										
Braconidae*	---	---	---	---	4/0.04	5/0.05	---	---	---	---
Formicidae*	---	6/0.06	---	---	4/0.04	9/0.09	---	---	---	---
Cynipoidea*	---	---	---	---	7/0.07	---	---	---	---	---
Chalcidoidea*	---	---	7/0.07	---	---	---	---	---	---	---
<i>COLLEMBOLA</i>										
Sminthuridae*	---	29/0.35	---	11/ 0.1	29/ 0.8	14/0.27	19/0.45	27/ 0.3	17/0.17	38/ 1.9
Entomobryidae*	---	29/ 0.5	14/ 0.4	---	15/0.18	---	3/0.03	---	---	50/ 1.1
<i>OTHER</i>										
Millipede*	---	---	---	---	---	5/0.05	---	---	---	---
Centipede*	---	---	---	---	---	5/0.05	---	---	---	---
Pelycepoda	---	12/0.12	---	---	---	5/0.05	---	---	17/ 0.3	13/0.13
Gastropoda	---	---	---	---	7/ 0.1	---	---	7/0.07	35/ 1.3	---
Oligochaete	---	---	---	---	---	---	---	7/0.07	---	---
Spider*	---	6/0.06	---	11/ 0.1	18/0.18	14/0.14	26/0.26	---	17/0.17	---
Mite	---	12/ 0.9	36/ 0.7	22/ 0.2	7/0.07	---	3/0.03	---	---	13/0.13
Nematode	---	---	57/ 0.4	---	7/0.07	---	---	---	17/0.17	---
Detritus	---	---	---	---	4/0.04	---	---	---	---	---

* No organisms were found in stomachs during December.

* Adult.

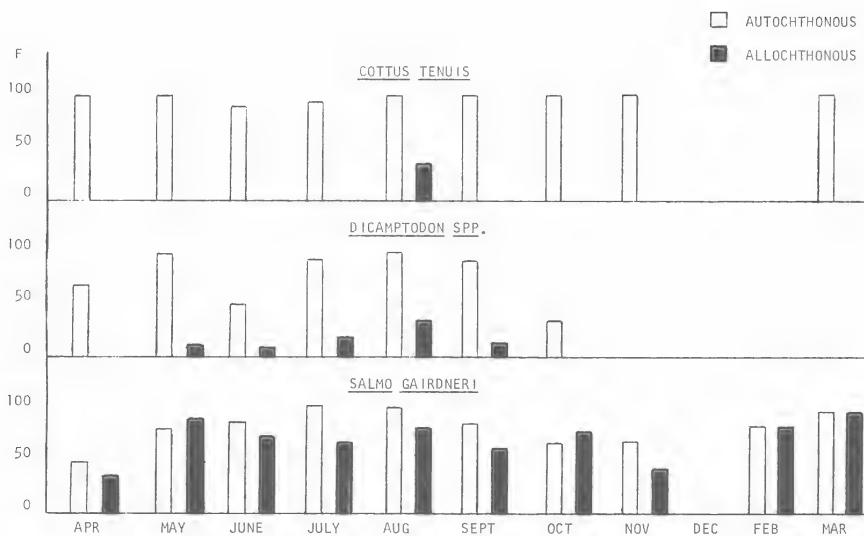


Figure 1. Frequency of occurrence of truly aquatic food items (autochthonous) versus that of emergent adults and nonaquatic organisms (allochthonous).

The data indicate that there is considerable overlap in the diets of the four animals studied. With the exception of *Cottus*, stream organisms are consumed relative to their availability. The overlap is not absolute. *Dicamptodon* spp. and *Cottus* are restricted largely to autochthonous organisms, while *Salmo* includes many allochthonous families. The fact that *Salmo* feeds on allochthonous organisms as well as stream staples suggests that *Salmo* has a relatively broad food niche. The seemingly selectiveness of the sculpin narrows its food niche considerably in comparison with the other two vertebrates. From these observations it seems that complete competition, at least in relation to food, is not occurring except perhaps in the case of *Cottus* whose selectivity may put it in the realm of complete competition with the other two vertebrates. *Salmo* and *Dicamptodon* show sufficient diversity in feeding habits to describe them as partial competitors. There were fewer sculpins collected than trout, and rareness may be an indication that they are having difficulty coexisting with the other species. However, at any time or place, disease, water temperature, lack of breeding sites, accidents, or any number of other variables could affect the density of the sculpins independent of the presence or absence of the other species. Since it is impossible to control all of these variables, except in very artificial circumstances, positive proof is probably unattainable. During the winter months, *Dicamptodon* spp. seemed to disappear from the stream. Assuming some kind of subterranean overwintering, this may be another manner in which complete competition is avoided by *Dicamptodon* spp.

Summary

Dicamptodon spp., *Salmo gairdneri*, and *Cottus tenuis* were collected from Maratta Creek at monthly intervals for one year. Examination of their stomach contents relative to availability of stream organisms indicates that feeding is, for the most part,

opportunistic. *C. tenuis* exhibits a degree of selectivity which may impose some competitive stress upon it. *Dicamptodon* spp. appears to feed almost entirely on benthos while *S. gairdneri* feed on organisms throughout the stream. The relative rarity of sculpins may suggest that competition with the other two vertebrates is approaching completion. Competition between *Salmo* and *Dicamptodon* spp. is relaxed somewhat by diversity of feeding habits and the probably subterranean habits of *Dicamptodon* spp. during part of the year. The feeding habits of the salmonid and salamanders suggest only "partial exclusion."

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Investigations Concerning the Taxonomic Status of the Sea Pen *Ptilosarcus gurneyi* (Cnidaria, Pennatulacea)

Introduction

Ptilosarcus gurneyi (Fig. 1) is found in the northeastern Pacific Ocean usually in a muddy or sand-mud substratum (Verrill, 1922; Deichmann, 1936). The species seems to be limited to a narrow band from about 3-135 m in depth with a latitudinal range from Alaska to southern California.

This sea pen has been described by numerous authors (Gray, 1860; Gabb, 1862; Moroff, 1902). Variations in color, among other features, have led to the assignment of different generic and specific names without clear evidence that different taxa were actually being described. The purpose of this paper is to investigate the validity of the existing taxonomic designations of the shallow water West Coast sea pen.

Sea Pen Nomenclature

The following is a list of taxonomic names which have been used to describe what is apparently a single species. A history of these nomenclatural changes is presented immediately following the list.

Sarcoptilus Gray, 1848.

Sarcoptilus (*Ptilosarcus*) *gurneyi* Gray, 1860.¹

Ptilosarcus Verrill, 1865.

P. gurneyi Verrill, 1865.

P. quadrangularis Moroff, 1902.¹

P. quadrangulare Flora, 1966.

P. guernei Deichmann, 1941.

P. verrilli Boone, 1933.

Leioptilus Gray, 1860.

L. guernei Flora, 1966.

L. quadrangulare Flora, 1966.

Leioptilum Verrill, 1865.

L. quadrangulare Kükenthal, 1913.

Leioptillum Verrill, 1868.

Liopitulum Kölliker, 1872.

Pennatula Linnaeus, 1758.

P. tenua Gabb, 1862.¹

P. tenuis Gray, 1870.

¹ = actual species description. Other authors and dates are given to show authorship of misidentifications or of misleading spelling variations.

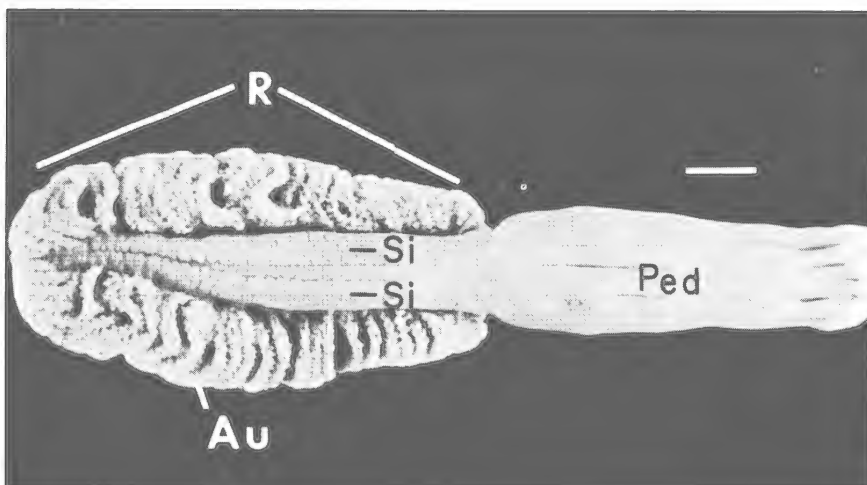


Figure 1. *Ptilosarcus gurneyi* showing peduncle (Ped), rachis (R), numerous autozooids (Au) at edge of leaf plates, and the two siphonozooid (Si) bands. Scale: 2 cm.

Gray (1848) described the genus *Sarcoptilus* which he later (1860) divided into two subgenera, *Sarcoptilus* and *Ptilosarcus*. He named two new species, *Sarcoptilus* (*Ptilosarcus*) *sinuosus* from New Guinea and *Sarcoptilus* (*Ptilosarcus*) *gurneyi* from Monterey Bay, California. He also named a new genus from Japan, *Leioptilus*. This latter animal was previously called *Pennatula fimbriata* Herklots, 1858, but was removed from *Pennatula* by Gray and the new genus established with *Leioptilus fimbriata* (Herklots, 1858) as the type species.

Subsequent spelling variations of *Leioptilum* (Verrill, 1865), *Leioptillum* (Verrill, 1868), and *Lioptilum* (Kölliker, 1872) were applied to this genus, but the first spelling of *Leioptilus* by Gray (1860) is the correct spelling of this genus (International Code of Zoological Nomenclature, 1964, art. 23).

In 1865 A. E. Verrill described a new species of sea pen he called *Leioptilum undulatum*, giving Gray credit for the generic name but using the neuter ending. Verrill also stated that the subgenera *Ptilosarcus* and *Sarcoptilus* were actually separate genera and listed the Monterey Bay specimen as *Ptilosarcus gurneyi*.

Gabb (1862) described a sea pen from the West Coast off Cape Flattery, Washington as *Pennatula tenua*. Gray (1870) listed Gabb's species as *Pennatula tenuis* and considered it as a complete synonym of *Ptilosarcus gurneyi*. The situation was further confused when Moroff (1902) described *Ptilosarcus quadrangularis* from Monterey Bay, California. He also suggested that *Ptilosarcus* and *Leioptilum* are not distinct enough to be separate genera. Later, Kükenthal (1913) suggested that the name *Leioptilum quadrangulare* be used for the California species and indicated that the name *Ptilosarcus* should be subordinated to the name *Leioptilum*. Conversely, Deichmann (1936) stated that *Leioptilus* is equivalent to *Ptilosarcus* but *Ptilosarcus* is preferred.

More recently, Flora (1966) listed, without discussion, the animal as *Leioptilus*

guernei = *Leioptilus quadrangulare* = *Ptilosarcus quadrangulare* = *Ptilosarcus quadrangularis*.

A question of priority, however, exists concerning the generic name *Leioptilus*. This name was published simultaneously by Gray (1860) for the sea pen and by Wallengren (1860) for a European plume moth (Lepidoptera, Pterophoridae) as cited by Neave (1939). However, Wallengren's article was actually published in October of 1859; Gray's article was not published until 1860. This gives Wallengren's genus *Leioptilus* priority, and, therefore, the name cannot be applied to the sea pen as Gray suggested.

Since later authors (Kölliker, 1872; Moroff, 1902; Kükenthal, 1911; Kükenthal and Broch, 1913; Kükenthal, 1915; Hickson, 1916) stated that the sea pen names *Leioptilus* and *Ptilosarcus* are synonyms, it is apparent that *Ptilosarcus* is the earliest valid generic name for the sea pen.

Moth Nomenclature

Zeller (1867) changed the spelling of Wallengren's genus of moth from *Leioptilus* to *Lioptilus*. However, Neave (1939) has indicated that the genus *Lioptilus* was already occupied by 1867, having been used by Cabanis in 1850 to describe a genus of bird. (Cabanis' *Lioptilus* is not to be confused with Blyth's (1847) *Leioptila* (= *Lioptila* Walden, 1875) a different genus of bird.) As a consequence, *Lioptilus* cannot be applied to the moth genus, emphasizing that *Leioptilus* is the correct spelling for the moth genus.

Forbes (1923), Essig (1926), Leonard (1928), and McDunnough (1939) all concurred in transferring the moth species of *Leioptilus* into the genus *Oidaematophorus* Wallengren, 1860, thus freeing *Leioptilus* for use as a generic name. By 1939, then, the use of *Leioptilus* as a genus of moth had been abandoned, making this name available for occupancy. If the sea pen genera *Ptilosarcus* (Gray, 1860) and *Leioptilus* Gray, 1860 are synonyms, then *Ptilosarcus* must be used as the correct generic name up to 1939 because of prior occupancy of *Leioptilus* by the moth. Although the name *Leioptilus* was available after 1939, *Ptilosarcus* must still be used as the correct generic name since *Ptilosarcus* was described prior to the date at which *Leioptilus* became available for occupancy.

Discussion

Gray's removal of *Leioptilus* from *Pennatula* was considered to be incorrect, based on two characters which he used to separate the two genera: (i) the leaf shape and (ii) the position of the siphonozooids. The leaf shape of *Pennatula* varies from a triangular shape to a sickle shape. The leaf shape of Gray's *Leioptilus fimbriata* (Fig. 2) is also sickle shaped. The siphonozooids of *Pennatula* extend from the dorsal tract out between the leaf plates. Gray's *Leioptilus fimbriata* (Fig. 3) has the same characteristic. Based on these characters, Gray's *Leioptilus* cannot be shown to be different from *Pennatula*. Species which were later incorrectly placed in *Leioptilus* clearly belong to *Ptilosarcus*. *Leioptilus fimbriata* should therefore be replaced by *Pennatula fimbriata* as originally described by Herklots (1858), and the remaining species of *Leioptilus* (*L. undulatum* Verrill, 1865) should be moved into *Ptilosarcus* (ICZN, arts. 23, 79).

Gray's genus *Leioptilus* has thus been shown to be invalid based on two different criteria: (i) homonymy (see introduction), and (ii) taxonomic synonymy.

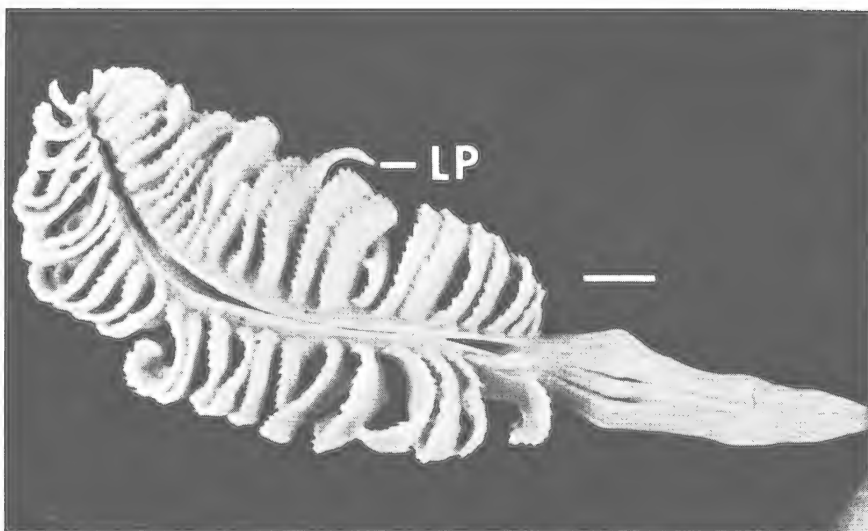


Figure 2. *Pennatula fimbriata* showing sickle-shaped leaf plates (LP) and ventral sulcus along length of rachis. Scale: 1 cm.

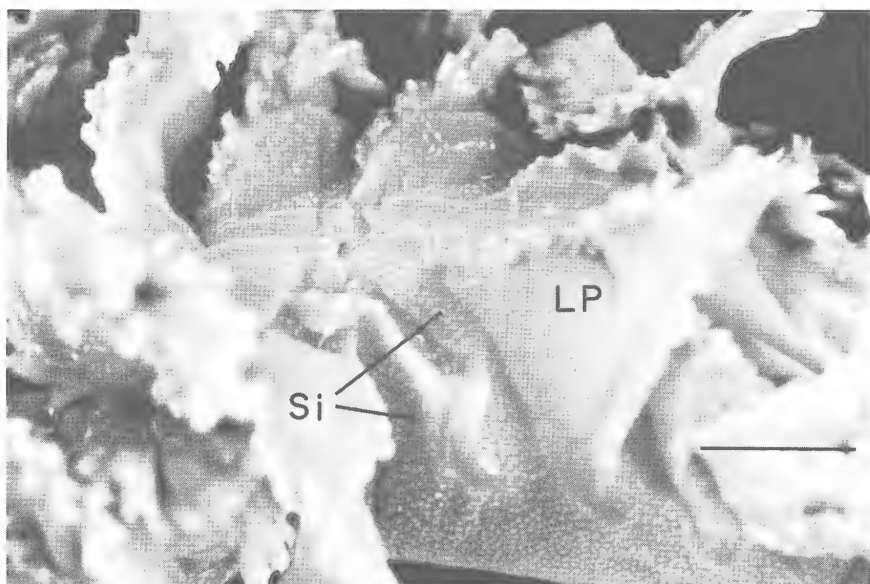


Figure 3. *Pennatula fimbriata* showing siphonozoids (Si) extending between leaf plates (LP). Scale: 0.5 cm.

The genus *Ptilosarcus* is the correct and valid generic name for the West Coast sea pen, two species having been described from the Monterey Bay region of California. The first, *Sarcoptilus* (*Ptilosarcus*) *gurneyi* Gray, 1860, is now validly called *Ptilosarcus gurneyi* since Verrill (1865) raised the subgenus *Ptilosarcus* to full generic status. The second is *Ptilosarcus quadrangularis* Moroff, 1902. However, from the description of the two type specimens, no significant taxonomic differences could be found to justify retention of *P. quadrangularis* as a separate species.

Gray (1860) described the new subgenus *Ptilosarcus* as having "Pinnules with a flattened, rather broad edge, spinulose on the margin; cells large, on the flattened edge surrounded with spicula. Stem $\frac{1}{2}$ the entire length."

He continued with a description of the new species *Sarcoptilus* (*Ptilosarcus*) *gurneyi*: "Orange. Pinnules smooth, very much crowded, closely imbricated, with a rather broad, distinctly spinulose edge. Cells crowded. Stem elongate, thick, half the entire length, much swollen above. California, Monterey. J. H. Gurney, Esq., M.P. Brit. Mus."

Moroff (1902) in describing the new species *Ptilosarcus quadrangularis* stated that the "Plant [sic] is slim, strong, dorsoventrally enclosed; stem comprises almost half of the plant [sic], is very thick, and above the middle has a strong swelling; feather is $2\frac{1}{2}$ times as long as it is wide; 54 leaves in all, semicircular, widely attached, close together, with many small lime needles under the skin; polyp area is 3-4 rowed, covered with strong needles; polyp calyces with two teeth; polyps without lime needles in the tentacles; ventral [sic] zooids are of a kind found on low warts; no lateral zooids; axis has four edges, is orange in color; chalk grains appear overall, orange in color."²

Because of the ambiguous descriptions, it was necessary to obtain the type specimen of *P. gurneyi* from the British Museum, and the type specimen of *P. quadrangularis* from the Munich Museum. Upon receipt of the animals from the British Museum, it was discovered that the animal from which the new subgenus and species were erected by Gray (1860) was mislabeled. The collection site, collection date, and the collector corresponded to the original published data, but the animal inside the jar was obviously not the specimen described by Gray. The mislabeled animal was identified as *Pteroeides breviradiatum*, a western Pacific species. The misplaced holotype of *Ptilosarcus gurneyi* was later found under the *Pteroeides breviradiatum* label, and, at the recommendation of the British Museum, both animals were properly relabeled.

The specimens from Munich were labeled as *Ptilosarcus quadrangularis* Moroff, 1902 and consisted of three syntypes in the same container—all three having a single label as "TYPUS." It is interesting to note from Moroff's species description (see above) that the sea pen had 54 leaves. None of the specimens labeled as the types, however, had this many leaf plates. One other specimen from the Munich Museum collection did have 54 leaf plates but it had no collection date or other data on the label other than *Ptilosarcus* sp. Thus none of the three animals labeled as "TYPUS" was actually described by Moroff as the type for the new species.

From the description of *P. quadrangularis* given by Moroff and from the comparison of other specimens of *P. gurneyi* from both museums (Table 1), it is apparent that *Ptilosarcus gurneyi* and *Ptilosarcus quadrangularis* are complete synonyms.

A comparison of the spiculae from the peduncle, siphonozooids, and the autozooids further emphasized that there are no taxonomic differences between the two. Both

² Translation from German by Karin Radtke.

TABLE 1. Comparison of taxonomic characters of *Ptilosarcus gurneyi* and *Ptilosarcus quadrangularis*.

British Museum Specimens	Color	Plate Number	Total length	Ped./Rachis ratio
<i>Ptilosarcus gurneyi</i> Holotype	orange	43	19.2 cm	9.2/10.0 cm
<i>Leioptilum quadrangularis</i>	red	30	12.5	5.3/7.2
<i>Leioptilum gurneyi</i>	brown	—	—	10.2/—
<i>Leioptilum gurneyi</i>	orange	52	25.6	12.9/12.7
Munich Museum Specimens				
<i>Ptilosarcus quadrangularis</i> Typus I	red to orange.	48	23.2	10.2/13.0
Typus II	red to orange.	33	13.9	7.0/6.9
Typus III	red to orange.	22	6.5	3.4/3.1
<i>Ptilosarcus gurneyi</i>	brown	53	15.6	6.5/9.1
<i>Ptilosarcus</i> sp.	orange	54	25.6	13.4/12.2
British Museum Specimens	Ped./Rachis fraction	Calyx #	Rachis Thickness	Width
<i>Ptilosarcus gurneyi</i> Holotype	.920	2	2.1 cm	3.7 cm
<i>Leioptilum quadrangularis</i>	.736	2	2.5	1.4
<i>Leioptilum gurneyi</i>	—	2	2.7	1.8
<i>Leioptilum gurneyi</i>	1.015	2	2.6	4.0
Munich Museum Specimens				
<i>Ptilosarcus quadrangularis</i> Typus I	.785	2	3.2	2.5
Typus II	1.013	2	1.7	1.2
Typus III	1.095	2	1.0	0.6
<i>Ptilosarcus gurneyi</i> *	.715	—	1.6	2.2
<i>Ptilosarcus</i> sp.	1.098	2	2.9	5.0

* Specimen appears to have been damaged when collected as there are no calyces present.

have rice grained-shaped, flat spiculae in the peduncle ($39\mu \times 78\mu$) and large tri-flanged spiculae from the autozooids and the siphonozooids ($47 - 78\mu \times 500 - 600\mu$). Both specimens had two well-formed calyx teeth, produced by the larger spiculae coming together to a pointed projection which arched over the autozooids. The only apparent distinction between the two specimens was that of color. All of the animals labeled *Ptilosarcus quadrangularis* TYPUS were reddish in color. This red color, however, does not seem to be a stable enough character on which to base species differences, as it is not always found uniformly throughout a colony. The edges of the leaves may be red without the peduncle being red, or the entire colony may be red. I have observed some colonies off the Oregon coast with partially red leaves, although the peduncle and the majority of the leaves were orange. It is not known whether this red coloration is seasonal, but it can be highly variable.

The similarity of anatomy, spicule shapes and arrangements, and the variability of color suggests that *Ptilosarcus gurneyi* and *Ptilosarcus quadrangularis* are complete synonyms. Since *P. gurneyi* was described in 1860 and *P. quadrangularis* in 1902, the name *P. gurneyi* has priority. The syntypes of *P. quadrangularis* should thus be considered as *P. gurneyi* topotypes. Therefore, based on earlier findings, it is apparent that *Ptilosarcus* and *Leioptilum* are complete synonyms, with *Ptilosarcus* the preferred name. It is also apparent that *Ptilosarcus gurneyi* (Gray, 1860) and *Ptilosarcus quad-*

rangularis Moroff, 1902 are complete synonyms. It is suggested that all of the species formerly allied with *Leioptilus* (except *L. fimbriata* which is a *Pennatula*) be now allied with *Ptilosarcus* and that *Ptilosarcus gurneyi* be used instead of *Ptilosarcus quadrangularis*.

A complete synonymy of the valid species of *Ptilosarcus* is quite complicated although there are apparently only three species: *P. gurneyi*, *P. sinuosus*, and *P. undulatus* (the species name here being a respelling of Verrill's *Leioptilum undulatum* to agree in gender with *Ptilosarcus*). A detailed history of the names applied to this genus and a review of its synonymy are presented in Appendix A. A taxonomic key to the genera of the Pennatulidae, including *Ptilosarcus*, is presented in Appendix B.

Acknowledgments

I wish to express my gratitude to Dr. P. F. S. Cornelius of the British Museum, to Dr. H. Fechter of the Munich Museum, and to Dr. K. Ruetzler of the National Museum of Natural History (Smithsonian Institution) for allowing me to study their priceless specimens, many of which are over 100 years old. I also wish to thank Dr. J. E. Morris and Dr. C. J. Bayne for providing many helpful suggestions in the preparation of this manuscript.

Appendix A

The following is an historical account of the different names applied to this genus (Appendix A Table 1). Appendix A Table 2 gives a synonymy of the different genera and species involved.

It is certain that *Pennatula tenua*, *Pennatula tenuis*, *Ptilosarcus quadrangularis*, and *Ptilosarcus verrilli* (Boone, not *P. verrilli* of Pfeffer) are junior synonyms of *Ptilosarcus gurneyi*. Similarly, *Leioptilus fimbriata*, *Leioptilus fimbriatus*, *Ptilosarcus grayi*, *Ptilosarcus brevicaulis*, *Pennatula sulcata*, and possibly *Ptilosarcus sinuosus* are junior synonyms of *Pennatula fimbriata*.

Ptilosarcus gurneyi (= *P. guernei*) (Boone, 1933, nov. *P. gurneyi* of Gray), *Leioptilum solidum*, *Ptilosarcus verrilli* (not *P. verrilli* of Boone), and *Ptilosarcus sinuosus* (not *P. sinuosus* of Gray) are all junior synonyms of *Ptilosarcus undulatus* (emend.).

Thus there seem to be three main areas of distribution of the genus *Ptilosarcus*: from Alaska to southern California (*P. gurneyi*), from the Gulf of California to Peru (*P. undulatus*), and from Australia and New Zealand (*P. sinuosus*, if this is different from *Pennatula fimbriata*).

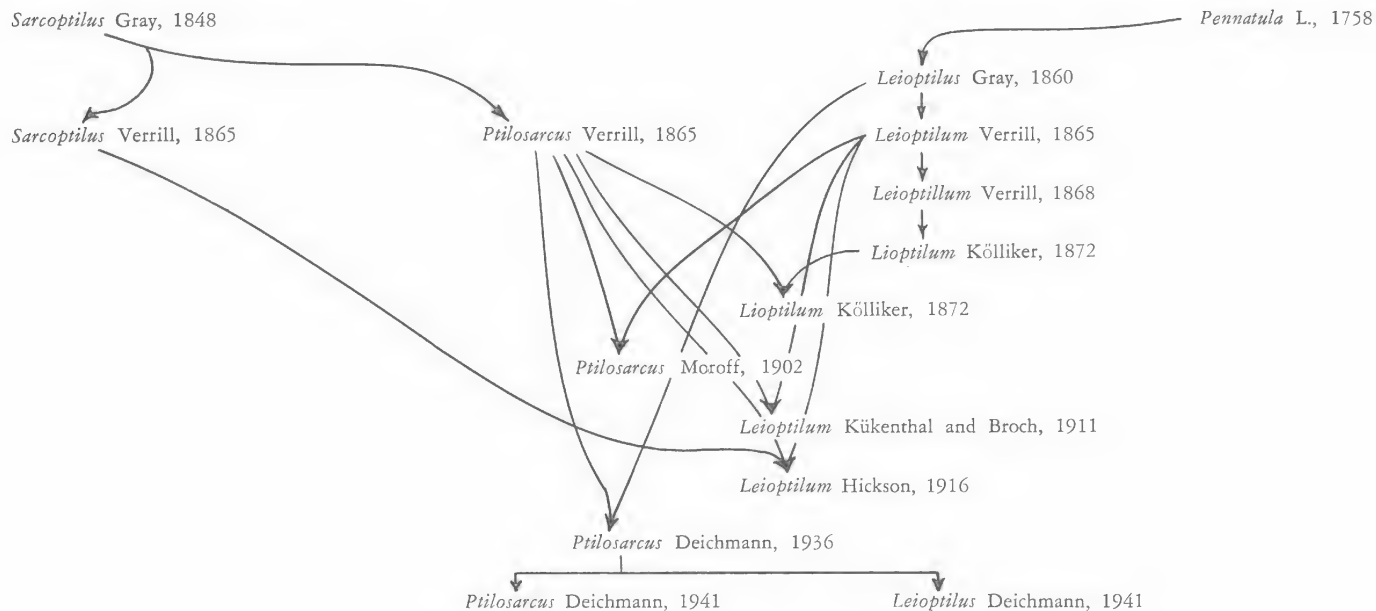
Appendix B

The following is a suggested key to the genera of Pennatulidae accompanied by a key to the species of *Ptilosarcus* found on the West Coast of the Americas:

(adapted from Hickson, 1916 and Deichmann, 1936)

- 1a. With large (300-600 μ .) tri-flanged spicules in the leaves. May be limited to edge or cover most of leaf surface. No spicules in tentacles of autozooids. 2

APPENDIX A TABLE 1. Synonymies of *Sarcoptilus*, *Ptilosarcus*, and *Leioptilus*. Arrows point from genera under consideration to combined genus with author and date following emended designation.



APPENDIX A. TABLE 2. Synonymies at species level. Arrows show from which genus new genus or subgenus is derived. Synonymous names are placed under oldest described name for that genus.

<i>Sarcoptilus grandis</i> Gray, 1848			<i>Pennatula linnaeus</i> , 1758
↓		↓	↓
<i>Sarcoptilus</i> (<i>Sarcoptilus</i>) <i>grandis</i> Gray 1860	<i>Sarcoptilus</i> (<i>Ptilosarcus</i>) <i>gurneyi</i> Gray, 1860	<i>Sarcoptilus</i> (<i>Ptilosarcus</i>) <i>sinuosus</i> Gray, 1860	<i>Pennatula fimbriata</i> Herklots, 1858
↓		↓	= <i>Leioptilus fimbriata</i> Gray, 1860
<i>Sarcoptilus grandis</i> Verrill, 1865	<i>Ptilosarcus gurneyi</i> Verrill, 1865	<i>Ptilosarcus sinuosus</i> Verrill, 1865	= <i>Leioptilus fimbriata</i> Gray, 1870
	= <i>Pennatula tenua</i> Gabb, 1862		= <i>Ptilosarcus grayi</i> K��lliker, 1872
	= <i>Pennatula tenuis</i> Gray, 1870		= <i>Pennatula sulcata</i> K��lliker, 1880
	= <i>Ptilosarcus quadrangularis</i> Moroff, 1902		= <i>Ptilosarcus brevicaulis</i> Nutting, 1912
	= <i>Ptilosarcus verrilli</i> Boone, 1933 (not <i>P. verrilli</i> of Pfeffer, 1886)		= ? <i>Ptilosarcus sinuosus</i> Deichmann, 1936
= <i>Leioptilum grayi</i> , Hickson, 1916			
	<i>Ptilosarcus undulatus</i> emend. Bate, 1972		
	= <i>Leioptilum undulatum</i> Verrill, 1865		
	= <i>Leioptilum undulatum</i> Verrill, 1868		
	= <i>Leioptilum verrilli</i> (Pfeffer, 1886)		
	= <i>Leioptilum solidum</i> Broch, 1910		
	= <i>Ptilosarcus verrilli</i> Pfeffer, 1886 (not <i>P. verrilli</i> of Boone, 1933)		
	= <i>Ptilosarcus gurneyi</i> Boone, 1933 (not <i>P. gurneyi</i> of Gray, 1860)		
	= <i>Ptilosarcus gurneyi</i> Boone, 1933 (not <i>P. gurneyi</i> of Gray, 1860)		
	= <i>Ptilosarcus sinuosus</i> K��lliker, 1872 (not <i>P. sinuosus</i> of Gray, 1860)		

- 2a. Leaves triangular, fan-shaped or sickle-shaped with long, prominent calyx teeth. Siphonozooids never on leaves, but may extend between leaves. *Pennatula*
- 2b. Leaves kidney-shaped, calyx teeth short and broad. Siphonozooids never extend between leaves but form two bands down dorsal tract of rachis, may be single or in clumps. *Prilosarcus* 3
- 3a. With two distinct calyx teeth. Orange to red in color. Siphonozooids not clumped. *P. gurneyi*
- 3b. With one distinct calyx tooth. Siphonozooids and dorsal tract red. Siphonozooids clumped. Calyx tooth yellow tipped. *P. undulatus*
- 1b. With large tri-flanged spicules forming fan-shaped support at base of leaves. Small (30μ) flat spicules in the calices, rachis, and tentacles. *Acanthoptilum*
- 1c. With small (50μ) flat spicules in the leaves. *Scytalium*

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Reactions of Canada Geese to Reservoir Impoundment on the Snake River in Washington

A difficult aspect of river-development evaluation is the effect of dams upon wildlife. Currently a vast network of moderately sized dams is being constructed in the Pacific Northwest. Many of these dams, such as those completed and being completed on the Snake River in southeast Washington, create profound changes in the ecology of the entire region. Unfortunately, the need for pre- and post-impoundment research on such areas is usually realized too late. Vast changes in ecosystems occur without meaningful studies being conducted.

This report is the latest of a continuous series of waterfowl studies, primarily concerning the great basin Canada goose *Branta canadensis moffitti*, conducted prior to, during, and after completion of a series of dams on the Snake River. Buss and Wing (1966) summarized pre-impoundment observations on nesting Canada geese and wintering mallards for the period 1954-1965. Culbertson *et al.* (1971) studied the same area from February 1966 through May 1968, reporting further information on nesting and behavior of Canada geese prior to completion of dam construction. Field work for the present study was conducted from August 1968 to August 1969 and from February 1970 to June 1970 while five remaining islands that had long been used for successful breeding were inundated.

The three objectives of this study are: (1) to evaluate ecological changes and their effects on Canada goose nesting on the Snake River between Almota and Central Ferry, Washington, as dam construction inundated important breeding sites, (2) to study various aspects of goose behavior based partly on marked geese, and (3) to study the use of artificial nesting structures under pre- and post-impoundment conditions.

The Study Area

The study area, which extended from near Clarkston at the Washington-Idaho line westward about 47 miles to Lower Monumental Dam, was divided into four units. Unit A (Fig. 1) extended from Wawawai to near Central Ferry bridge, a distance of approximately 16 miles. Nesting studies have been conducted in this unit since 1954. The five remaining islands in this stretch of the river were inundated in February 1970.

Unit B (Fig. 1) extended 14 miles downstream from Central Ferry bridge to Little Goose Dam. Because geese tended to concentrate in Unit B, this stretch of river was utilized in June and July 1969 for capturing and marking geese. In the spring of 1970 brood behavior was observed in this unit.

Unit C (Fig. 2) extended from Lower Monumental Dam 15 miles upstream to

Lyons Ferry. Unit D (Fig. 1) was a three-mile length of river beginning 8 miles downstream from Clarkston. These two units were used for the study of artificial goose nesting structures.

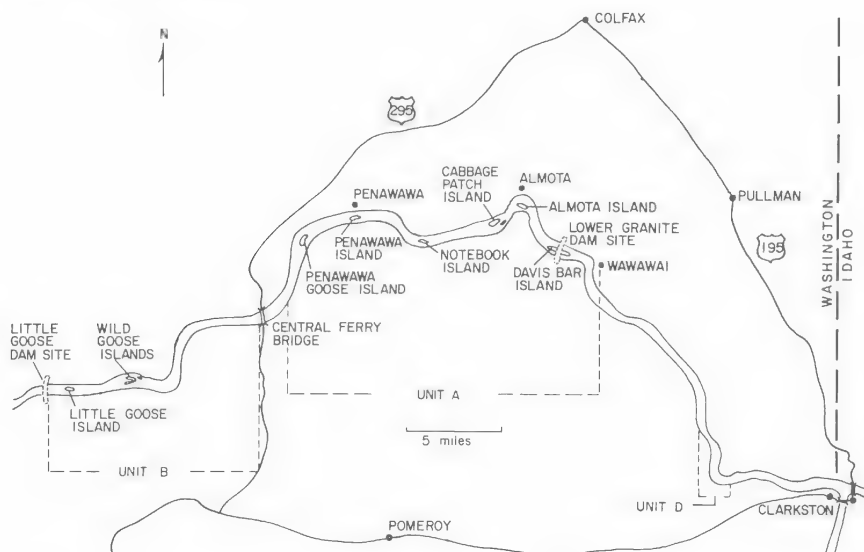


Figure 1. Map of the Snake River before February 1970.

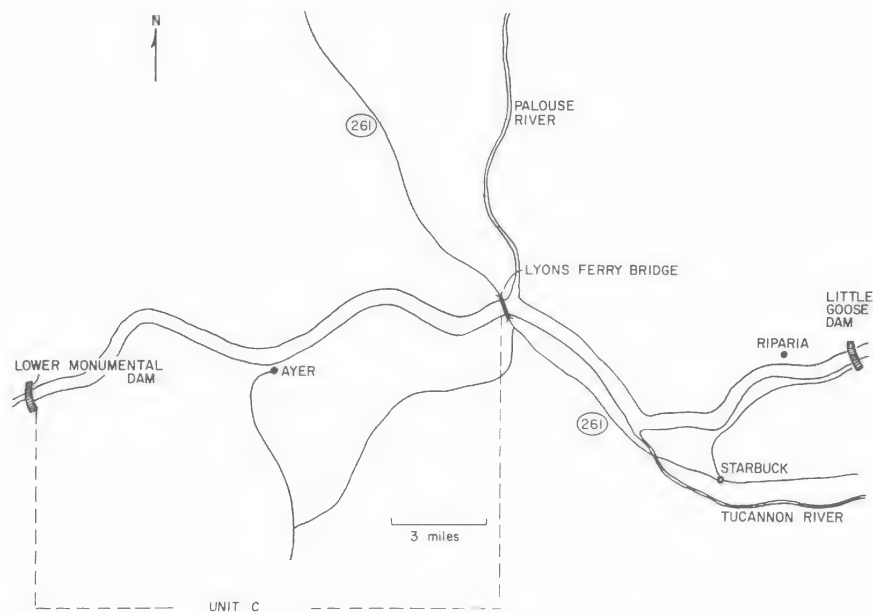


Figure 2. Map of Lower Monumental Reservoir on the Snake River.

The Snake River in southeast Washington flows through a basalt canyon with steep sides that drop 1000 to 2000 feet from the Palouse Plateau. This plateau is covered by light brown loess, underlain by many layers of basalt. Although agricultural development did not begin until about 1890, its expansion has been so rapid and intensive that few remnants of the original *Agropyron-Poa* climatic vegetation remain (Daubenmire, 1942).

Like the Palouse Plateau above, the floodplains and the more accessible islands and lower slopes of the Snake River Canyon have been utilized for agriculture. Wide-spread overgrazing has led to the replacement of the characteristic *Agropyron-Poa* climatic climax by cheat grass *Bromus tectorum*.

Generally, 65 to 70 percent of the total annual precipitation occurs from October to March, inclusive. Twenty inches occur at Clarkston. As the canyon winds farther west, precipitation declines gradually as a result of the rainshadow effect of the Cascade Mountains.

Both slopes of the Snake River Canyon are interrupted by many side canyons containing intermittent streams. The winding course of the river results in many wide bends, each typified by a steep basaltic slope on the outer side and a floodplain on the inner side.

Until completion of Lower Monumental and Little Goose dams the river was fast-flowing with a width of 100 to 800 feet. Since completion of the dams, the resulting reservoirs are up to three-fourths mile in width. Most of the original floodplain area has been inundated.

Before February 1970, five permanent islands existed in Unit A. These islands were low and elongated in the direction of the current. The upstream ends were low, rocky, and with sparse vegetation, whereas the downstream ends tended to be higher, with a relatively thick layer of silt. (For more complete descriptions of the area and islands see Buss and Wing, 1966, and Culbertson *et al.*, 1971.)

Methods and Materials

Nesting studies began in Unit A during the first week of March 1969. Three men walked abreast and searched along parallel transects from one end of an island to the other until the entire island was surveyed. The distance between individuals varied depending on vegetational density. In 1970, when only three small islands existed in the study area, a similar technique was used on selected areas of the shoreline. Data on location, clutch size, immediate vegetation, and history of each nest were recorded. Number, location, and behavior of all geese seen during field trips were also recorded.

Because geese were observed in small, scattered groups that showed no consistent patterns of movement, feeding, or other activity, capture techniques were restricted to hand-catching with a fisherman's landing net. Flightless geese were located from a boat. If they were on shore, they were chased inland on foot and captured where little cover was available. If geese were seen on water, an attempt was made to isolate and capture an adult. Usually after such a goose was pursued briefly, it would head for land where it was easily captured. After capture, age and sex of geese were determined according to criteria used by Hanson (1965) for *B. c. maxima* and *B. c. interior*. Since temperatures were high (100-120° F.) captured geese were marked, banded, and released immediately to minimize the danger of heat prostration. Each goose was banded with a no. 8 U.S. Fish and Wildlife Service legband and an

orange flexible plastic collar as described by Sherwood (1966). Culbertson *et al.* (1971) utilized a combination of bands, circles, and triangles marked on collars for rapid field identification. This method was also used in the present study. These geometric symbols, however, were difficult to distinguish at long ranges and, for people unfamiliar with the symbols, were difficult to interpret. The last two geese caught were marked with collars carrying arabic numbers.

An artificial nesting structure (Fig. 3) consisted of a 50-gallon drum split lengthwise, the two halves placed side-by-side, and angle iron welded across the tops of the ends. The inner side of each half was cut along the edges, flattened so that the two inner sides overlapped, and welded to form a "box" 34 by 45 by 12 inches. Three 18-inch sections of 2.5-inch diameter pipe welded to the box in a triangular pattern and braced by angle iron served as holders for 10-foot legs of 2-inch diameter pipe. A 12-by-12-inch plate was attached to one end of each leg. Four 1-inch drainage holes were drilled through the bottom of each box.

The split-drum of this design is large compared with those of several other designs. Although reduction in size would result in decreased costs and easier handling, the relatively large size is an important factor affecting use for nesting (Rienecker, 1971). Thus any advantages connected with reduction in size could be offset by a decrease in nesting use. The drums were generally filled to one-third of their depth with native grasses and/or hay. The nesting material was tightly packed to minimize wind losses. Many different nesting materials have been used by other investigators Craighead and Stockstad (1961) utilized soil or duff. Dill (1964) advocated hay or marsh vegetation, whereas Brakhage (1965) used sawdust topped with straw. Will and Crawford (1970) found prairie hay satisfactory, but regarded coarse wood shavings as far superior. They stated that wood shavings "shed water rapidly, are extremely water resistant, and in most cases need not be replaced for 3 or 4 years."

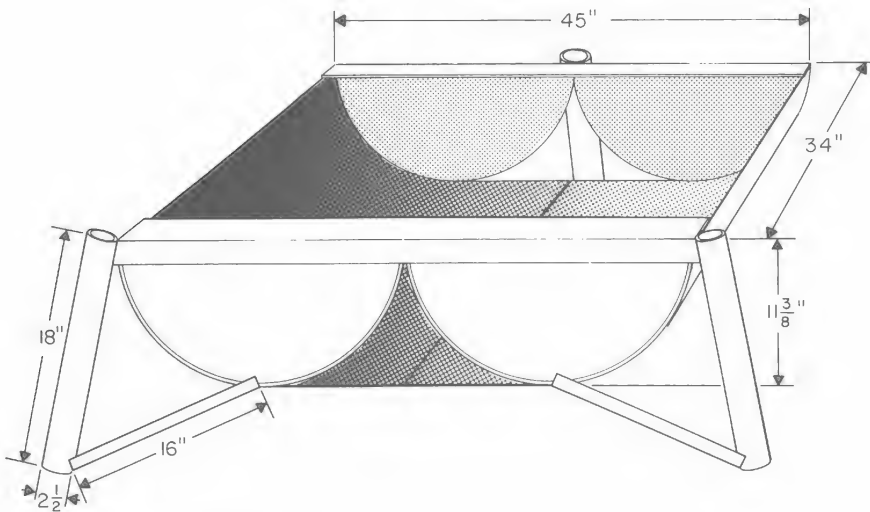


Figure 3. Artificial nesting structure.

Artificial eggs placed on the nest fill have been used successfully to attract geese to nesting structures (J. Stout, unpublished data). Such a technique may be particularly valuable in areas with no history of artificial-structure nesting.

Besides an arbitrary division of 20 structures each on Lower Monumental Reservoir and the free-flowing river in Unit D, structure sites were selected for isolation from human disturbance, practicality for structure placement, and ease of approach for observation. Structures were located no more than 100 yards inland or more than 10 yards into water. No two structures were placed closer than 100 yards apart to avoid intraspecific strife (Will and Crawford, 1970).

The drums were originally checked by use of a ladder, a procedure which was awkward, cumbersome, but reliable. A small mirror attached to a 6-foot pole and used to check for nesting activity was also used but proved unreliable.

Effects of Inundation on Nesting

Population Trends. Counts of geese have been made during the nesting season in Unit A almost continuously since 1954. For 1965, an average of 157 geese per trip was observed between February 27 and May 15, based on seven trips. In 1967, 11 trips between February 26 and May 21 resulted in an average of 97 geese, and in 1968 eight trips between February 29 and May 16 showed an average of 80 geese (Culbertson *et al.*, 1971).

Table 1 presents results of the present study. In 1969 an average of 90 geese per trip was observed, and in 1970 the average per trip was 89 geese. Culbertson *et al.*

TABLE 1. Numbers of geese seen in Unit A on river surveys.

1969	No. Geese	%	1970	No. Geese	%
Mar. 1	281	62.3	Mar. 7	169	37.8
Mar. 22	108	23.9	Mar. 21	102	22.8
Apr. 20	38	8.4	Apr. 4	51	11.4
May 4	10	2.2	May 2	72	16.1
May 18	14	3.1	May 16	53	11.9
Total	451			447	
Mean	90			89	

(1971) and Barraclough (1954) found that approximately 40 to 50 percent of the geese observed were involved in breeding. Ten nests were found in 1969, and three were found in 1970. Thus, only about 20 to 25 percent and 4 to 6 percent of the geese observed in 1969 and 1970, respectively, were involved in breeding. Assuming that a similar percentage of nests were not found each year, the ratio of the year-to-year percentages of geese involved in nesting should remain relatively constant.

Culbertson *et al.* (1971) observed that during the last two trips in 1968, on April 28 and May 16, the highest pair counts were made. They suggested that geese had been nesting on the cliffs or shoreline adjacent to the river, and were counted only after they brought their newly hatched goslings to the river. No post-hatching increase in number of geese was observed in 1969 and 1970. Instead, the maximum numbers of geese (including pairs) were observed in March, followed by a decline in numbers through April and May (Table 1). Couseland *et al.* (1960) and Couseland *et al.* (1961) worked on this area and observed maximum numbers in March and

April, respectively, with a consistent decrease in number of pairs through April and May.

Island Nesting. In 1969, 10 nests were found on the five islands in Unit A (Table 2). This was the lowest number of nests found since the study began in 1954.

TABLE 2. Summary of data for 320 goose nests for 16 years, 1954-1970.

Year	Total Nests	Average Clutch	Nests Hatched	Nests Abandoned	Nests Destroyed	Eggs Hatched	Eggs Abandoned	Eggs Destroyed	Total Eggs ^a	% Nests Hatched	% Eggs Hatched
1970	3	6.0	3	0	0	17	1	0	18	100	94
1969	10	5.0	6	4	0	32	18	0	50	60	64
1968	20	6.2	11	4	5	57	21	17	108	55	53
1967	29	4.8	9	8	12	48	42	50	140	31	34
1966	30	5.5	25	3	2	123	27	14	164	83	75
1965	30	5.7	19	2	9	100	28 ^c	48	176	63	57
1964	16	6.4	15	0	1	84	12	7	103	94	82
1963	18	6.1	14	3	1	86	17	6	109	78	79
1961	20	6.2	18	1	1	108	4	5	124	90	87
1960	19 ^b	5.4	14	0	2	69	3	11	95	74	73
1959	23 ^b	6.2	12	4	4	72	31	24	143	52	50
1958	29	5.5	18	0	11	101	4	40	145	62	70
1957	17	6.5	16	1	0	87	24	0	111	94	78
1956	18	6.2	13	0	5	76	0	35	111	72	69
1955	18	5.5	10	6	2	52	26	13	99	56	53
1954	20	6.5	17	2	1	97	22	6	125	85	78
Totals	320		220	38	56	1209	280	276	1821		
Aver.	20	6.0	13.8	2.4	3.5	75.6	18.8	17.3	113.8	69	66

^a Some totals include eggs unaccounted for.

^b Totals include three nests which were still under incubation at end of observation period.

^c Of these 28 eggs, 16 were infertile, 6 contained embryos, and 6 were undetermined.

Possible reasons for the low number found in 1969 are: (1) excessive human disturbances prevented geese from nesting, (2) high water inundated most of the suitable nesting habitat, or (3) low numbers of breeding pairs were available as a result of high adult mortality in previous years.

Excessive disturbance is by far the most probable cause for the small number of nests in 1969. The entire north bank of the river bordering Unit A was intensely disturbed by relocation of the Camas Prairie Railroad to a higher level in preparation for the flooding of Little Goose Reservoir. Also, an extensive length of the north bank was "rip-rapped." Heavy machinery operated along most of the north bank; blasting was not uncommon. From March 1969 onward through the nesting season construction work was continuous throughout the week, including Sunday.

In Table 3 data on mean number of nests per island during the 1954-1969 period and the 1969 deviation from the mean are presented. The greatest deviation occurred for Almota and Penawawa islands, which were close to areas where blasting was frequent. Although Penawawa Goose Island, which was directly adjacent to an area of heavy construction work, showed only a slight decrease from the mean, three of the four nest desertions observed in 1968 occurred on this island.

TABLE 3. Mean number of nests per island during 1954-1968 and 1969 deviation from mean.

Island	1954-1968 Mean No. of Nests	1969 No. of Nests	1969 Deviation from 1954-1968
Almota	5.4	1.0	-4.4
Notebook	1.3	0	-1.3
Cabbage Patch	1.2	1.0	-0.2
Penawawa	3.7	1.0	-2.7
Penawawa Goose	8.0	7.0	-1.0
Totals	19.6	10.0	-9.6

In 1970 only three small islands existed in Unit A. One nest was found in the middle of the largest of these islands.

Clutch Size. In Table 2 nesting data are presented for 1969 and 1970, and compared with those from 14 previous years. In 1969 the average clutch size for 10 nests was 5.0; the number of eggs per nest varied from two to nine. Geis (1956) in the Flathead Valley, Montana, and Hanson and Browning (1959) on the Hanford Reservation, Washington, reported averages of slightly over five eggs per nest. Data obtained since 1954 for the Snake River Canyon indicate that the average clutch size ranged from 4.8 eggs (1967) to 6.5 eggs (1957), with an overall average of 6.0 eggs per nest for a 16-year period. Thus the average clutch size for 1969 is near the lowest average for the area.

In 1970, one island nest (7 eggs), one cliff nest (6 eggs), and one artificial-structure nest (5 eggs) were found for an average clutch size of 6.0.

Hatching Success. Thirty-two of 50 eggs found in 1969 hatched (Table 2), a hatching success of 64 percent. The overall average for the 1954-1970 period was 66 percent. For successful nests, Geis (1956), Hanson and Browning (1959), and Steel *et al.* (1957) reported 85, 92, and 91 percent, respectively.

Five nests (1969) having a clutch size of five or more eggs produced 36 eggs of which 23 (64%) hatched; five nests having a clutch size of less than five eggs produced 14 eggs of which 9 (65%) hatched. Geis (1956) observed that older geese usually produce larger clutches. These data suggest that older pairs were no more successful in hatching than younger pairs. When the number of goslings produced by the two groups is considered, however, the nests having a clutch size of five or more eggs produced 72 percent of the goslings, but the nests having a clutch size of less than five eggs produced only 28 percent of the goslings. If the assumption that those geese producing five or more eggs were relatively old is correct, the importance of an adequate number of older pairs in the population is evident.

In 1970 three nests produced 18 eggs, of which 17 hatched for an overall hatching success of 94 percent. The egg which did not hatch was infertile.

Nesting Success. Nesting success (percentage of total nests hatching some or all of their eggs) was 60 percent (6 out of 10 nests) for 1969 (Table 2). For the 16-year period since 1954, 69 percent (220 of 320 nests) were successful. Generally, a nesting success of 70 percent or greater can be expected (Hanson, 1965; Miller and Collins, 1953; Naylor, 1953; Steel *et al.*, 1957). The 60 percent success for 1969 is well within the range of the previous 14-year period (31 to 94 percent).

In 1970 all three nests found hatched, or a nesting success of 100 percent (Table 2).

If the nesting data for the 15 years from 1954 through 1969 are examined closely, the annual number of nests suggests a bimodal distribution (Table 2). Grouping occurs around 18 (10 to 23) and around 29 (29 to 30). If the nesting success for these two groups is calculated separately, the low group (11 years) gives an average nesting success of 74 percent, whereas the high group (4 years) gives an average nesting success of 60 percent. A probability value calculated from the data presented in Table 2 under columns labeled "Total nests" and "Nests hatched" results in a p value of $<.04$. These calculations indicate that nesting success is higher in years with fewer nests than in years when large numbers of nests are present. Thus a density-dependent mechanism of controlling population is involved, as suggested by Buss and Wing (1966). Figure 4 is a graphic presentation of these data.

Causes of Nest Failure. Four nests were deserted in 1969. No nests were destroyed by predators or scavengers, even after several of the nests had been abandoned for several weeks. In comparison, five nests were destroyed by predators or scavengers in 1968 (Culbertson *et al.*, 1971).

During field trips in 1969, a few magpies *Pica pica* and ravens *Corvus corax* were observed along the banks. However, none was observed on the islands. Tracks of

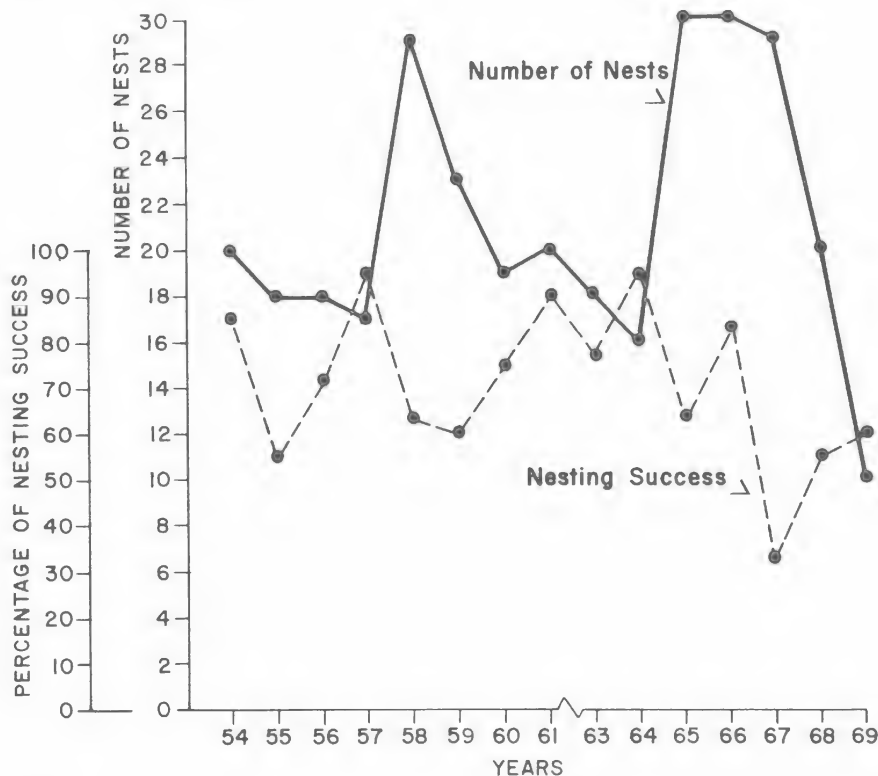


Figure 4. Number of nests and percentage of nesting success for 317 nests observed on six islands of the Snake River, 1954-1969.

either coyote *Canis latrans* or dog *Canis domesticus* were found on Almota Island, and several sets of raccoon *Procyon lotor* tracks were observed on Penawawa Island. No other evidence of predators, other than humans, was found.

Several reasons for desertion have been offered: (1) human interference (Geis, 1956), (2) nesting density (Munroe, 1960), and (3) intraspecific strife (Hanson, 1965). Culbertson *et al.* (1971) suggested that data available for Unit A indicated that desertion was probably caused mostly by human interference. Observations made during 1969 support the premise that human interference was the major cause of nest desertion in Unit A.

Direct human interference in 1969 seemed minimal when compared with that of previous years. Fishermen were observed on Almota and Penawawa Goose islands, and indirect evidence was found of people visiting the islands. As stated above, however, indirect interference by construction work along the north bank of the river was excessive. Two islands, Almota and Penawawa Goose, were closer than the other islands to the heaviest construction work. Almota Island showed a decrease in number of nests (Table 3), and Penawawa Goose Island had 75 percent (3 out of 4) of the total nest desertions in 1969.

Although large numbers of magpies and two raven nests were observed along the shores during spring 1970, none of the three nests found that year was destroyed or deserted.

Buss and Wing (1966) found single goose eggs at the lower and upper ends of Davis Bar on March 24, 1963, and a single egg on Almota Island on May 3, 1964. The eggs were not in or near a nest and were apparently laid at random. Culbertson *et al.* (1971) reported a single goose egg on Penawawa Goose Island on March 25, 1967, and another single on the same island on May 7, 1967. They considered the eggs laid in 1967 to be nesting attempts.

On May 1, 1969, a single egg was located at the extreme downstream end of Notebook Island, lying on smooth sand. On April 20, three single goose eggs were found scattered over Notebook Island, with no apparent relationship to any type of terrain or nest. Collias and Jahn (1959) and Munroe (1960) suggested that such single eggs are laid by females unable to find suitable nesting sites. During the spring of 1969, Notebook Island had no nests, even though conditions, except perhaps for disturbance caused by construction work, seemed suitable. The explanation proposed by Kossack (1950) that such eggs are a result of promiscuous laying seems very appropriate to the conditions observed. However, the possibility that unobserved disturbance made Notebook Island untenable to geese must be considered.

Nonisland Nesting. When the five islands in Unit A became inundated during February 1970, research emphasis shifted from studies of geese nesting on islands to those selecting nonisland sites. Would cliff and shoreline nesting increase, or would most breeding geese seek nesting sites in other areas? These were questions which were now primary targets for study.

Cliff nesting along the Snake River has been known for over 20 years (Jewett, 1949). Between 1947 and 1953, Yocom (unpublished data) found several goose nests located on the ledges above the river. Cliff nest sites have been reported at several locations in Unit A. In May 1957, five goslings hatched from a nest 200 feet above the river and near the upstream end of Almota Island (Fergin *et al.*,

1958). On April 30, 1967, a goose was observed leaving a shallow cave one mile upstream from Almota Island. An old nest hollow was found in the cave, and a recently dug nest pit was found 50 yards away on the same ledge. Although the ledge was searched later in the nesting season, no nest was found. Geese have been reported loafing on bluffs near Wawawai, Davis Bar Island, and Notebook Island (Culbertson *et al.*, 1971).

Few observations of river-bank nesting have been recorded. In 1960, when the Corps of Engineers began construction on Davis Bar Island, two nests were found on the river bank downstream from the island (Couseland *et al.*, 1960). A river-bank nest was observed two miles above Steptoe Canyon upstream from Unit A, in 1969.

The difficulty of finding goose nests, even under favorable conditions, should not be underestimated. For example, during a nesting survey conducted by personnel of the Washington Department of Game, New York Bar Island (several miles below Unit A) was systematically searched. This island, which is large but sparsely covered by vegetation, supported five nests in 1970. Although personnel conducting the search were experienced and weather conditions were favorable, two nests were missed. Likewise, some island nests were probably missed during annual nesting surveys conducted since 1954.

Although much time was spent by two separate field teams searching for cliff and shoreline nests in 1970, only two such nests were found. One of the nests, located on an artificial-nesting structure, is discussed below. The other nest was found independently and within a few days' time by both teams. The nest was constructed in a shallow cave on a narrow ledge about 50 feet above water (Fig. 5) on the south shore of the reservoir approximately a half mile from the former site of Cabbage Patch Island. The long time spent searching for the two nonisland nests and the extensive area searched support the conclusion that very few geese nested in the area during 1970.

Goslings were observed during the seven trips made from Wawawai to Penawawa Goose Island in April and May. The maximum number observed on any one trip was 23, recorded on May 16. These 23 goslings were only 6 (26 percent) more than the 17 that hatched from known nests. Culbertson *et al.* (1971) concluded that 50 to 60 percent of the goslings produced in Unit A came from nonisland nests. The very low maximum number of goslings seen on the study area in 1970 and the low percentage (probably representing only one brood) not accountable to a known nest also support the conclusion that very few geese nested in the area during 1970 and attest to insignificant production of geese from nonisland nests.

The decrease of gosling production following inundation suggests that preferred nesting sites were eliminated. Culbertson *et al.* (1971) observed 69 goslings on one trip through the same area that produced a maximum of only 23 goslings in 1970.

Both cliff and river-bank nests seem to be of minimal importance at present, but such nests may have been of more importance in the past. Although the cliffs on the south side of the canyon have been relatively undisturbed, the north slope has had many cliff areas ripped away to allow railroad relocation. In the process, many potential and actual sites were probably destroyed.

Behavioral Observations

Movements of Marked Geese. Geese have been marked in the study area since 1966, either with vinyl-coated nylon collars or flexible plastic collars. A goose marked with



Figure 5. Photograph of Canada goose nest on pinnacle of rock about 20 feet above water, about 70 miles upstream from Clarkston in Hell's Canyon (photo by Annette Tussing).

a plastic collar in 1968 was subsequently identified as the male of a pair that nested on Almota Island in 1969. One or more geese marked with a plain orange plastic collar in 1968 were seen in the study area in autumn 1968 and 1969, and spring 1969 and 1970.

Hand-catching immature geese caused some concern that family groups might be broken up. On July 3 four geese of a group of six were marked; on July 7 the four marked geese were seen in a group of six located a half mile west of the banding site. Four geese were marked from a group of seven on July 7; three of the marked birds were seen in a group of six on July 12 near the banding site. Marked geese were observed in the area until the end of July, when observation was discontinued until September.

During fall 1969, summer-marked geese were seen on two occasions. Hunting-season recoveries were obtained from two geese banded during the summer. One was shot near Washtucna, Washington, about 15 miles north and 15 miles west of the banding site on January 17, 1970; the other was shot within a half mile of the same site about a week later.

Collectively the observations on marked geese support the suggestion of Culbertson *et al.* (1971) and Hansen and Oliver (1951) that the Canada goose *B. c. moffitti* in south-central Washington is a permanent resident and that at least part of the population winters within 50 to 100 miles of the study area.

Attempts To Establish Territories. Very few of the 447 geese observed in the study area during 1970 (Table 1) succeeded in establishing territories. Their failure in territorial establishment is paramount to understanding the drastic decline in nesting and gosling production reported above.

The water level behind Little Goose Dam was raised during February 1970. On February 13 the highest parts of Penawawa Goose Island were above water, but this remaining area was small. Approximately 125 geese were in the water within 100 yards of the western end of the island.

In two hours of observation a minimum of three pairs and a maximum of seven pairs of geese were on the two remaining island remnants. Both the number and composition of pairs were constantly changing. Aggressive displays, consisting of lowered head and neck and erection of feathers, occurred infrequently, and displays were of short duration. Pairs wandered over the island remnants and entered and left the vicinity of groups of unpaired geese, seemingly at random. No unpaired geese were observed to approach the remaining island areas.

The water level of Little Goose Reservoir fluctuated 4.25 feet (at the site of Lower Granite Dam) until the middle of April. From the middle of February until the middle of April, the highest part of Almota Island and another island created by the raised water level about one-third mile upstream from Almota Island were alternately submerged and emerged. While these two islands were emergent, pairs of geese attempted to establish territories on them.

On February 21 and 23, a pair of geese was observed on Almota Island. After the island had been submerged once, however, only a group of five was seen on one of numerous trips past the island.

Before the island formed by raised water level was submerged the second time, observations revealed at least one pair and frequently two pairs of geese. When two pairs were present, they were at opposite ends of the island, and no interaction between the pairs was observed. Both pairs were reluctant to fly when closely approached by boat. When only one pair of geese was seen and closely approached, both members of the pair faced the boat, extended neck and wings vertically, erected feathers, and honked frequently. A search of the island disclosed no signs of nesting activity.

During the spring of 1970, pairs of geese were observed at various locations in Unit A. In at least three cases a pair was consistently found at the same location throughout the day and was reluctant to fly. Although each location was checked several times, no signs of nesting activity were ever found. These three pairs did not exhibit true territorial behavior, even if territorialism is broadly defined as the defense by a gander of an area around his mate.

For example, one pair was consistently found on a gently sloping meadow two miles east of Penawawa. Only once was another goose observed within 200 yards of the pair. On March 30, the pair was sitting at their customary location when a single goose approached and landed within five feet. The pair immediately flew about 25 feet and landed 10 feet apart. The single approached to within five feet of the nearest goose, which then flew about 10 feet back to its mate. During the next hour the single made no further attempts to approach the pair, and all three geese fed. The distance between the pair and the single varied from about 10 to 75 feet. No honking or aggressive displays occurred.

Sherwood (1967) observed that pair bonds often occur in yearlings, and stated that "the ardor of pair bonds in most yearlings started to wane after five or six weeks." Perhaps these three pairs of geese were yearlings only tentatively paired, thus accounting for their apparent lack of territorial behavior.

The observations of paired geese attempting to establish territories indicate that most of them failed and that partial or complete flooding of potential territories was responsible for their failure.

Interactions near Nests. Observations of geese near nests were recorded to supplement other behavioral observations, and hopefully help clarify reactions of geese to impoundment. When a boat passed the cliff nest, the goose made little or no attempt to conceal her position. Usually her neck was held almost in a horizontal position, and she followed the progress of a boat by merely bending her neck in a horizontal plane.

When the nest was approached on April 9, the goose was observed on the shelf outside the nesting cave. The gander was sitting approximately 10 feet above the cave entrance. Both geese were facing another pair of geese 30 yards away on the same level. The individuals of the second pair were sitting within five feet of each other. The pairs seemed more interested in each other than in the boat, which approached closely. Subsequently, during 30 minutes of watching from several hundred yards, the geese were quiet, moved very little, and showed no aggressive behavior. All four geese were gone when the nest was visited two hours later. The eggs were warm and covered with down. Although the nest was visited at least twice a week, only once was the goose away from the nest.

Rationalization of this behavior is speculative. Dow (1943) observed that if a pair of geese lost a nest and eggs, they may approach a "going" nest. Such an approach may result in fighting. Dow (1943) observed ganders fighting over nests and recorded nine nest desertions which apparently resulted from such fighting.

On May 4, 1970, a goose nest containing seven eggs was discovered on 0.25-acre Penawawa Bar Island, about a mile west of the former site of Penawawa Island. The goose flew when the nest was approached and landed in the water between the island and shore. The gander swam along the shoreline about 400 yards from the island. The goose swam to shore about 400 yards from the island; the gander swam to her position, leaving the water less than five feet from her.

After the boat left, the pair reentered the water and swam along the shoreline in the direction of the island, honking frequently. After swimming a short distance the pair flew 50 yards and landed closer to the island, where they were joined by a single goose. The three geese swam at intervals of about three feet; the rate of honking increased.

After about five minutes the three geese flew over the island and landed in the water on the opposite side. Then they swam slowly around the island, landing on a small sand bar on the inshore side. The single stayed closer to the gander than the goose, but immediately after landing the gander faced the single and assumed a head-down threat posture. The single assumed the same posture, but on the first lunge by the gander the single flew and landed within a few feet of the goose of the pair. She seemed to ignore the single. When the gander approached and drove the single into the air again, the single simply landed on the other side of the goose. The same pattern was repeated. When the single flew for the fourth time, the gander

followed it into the air and chased it for about 100 yards. The single landed and stayed in the water close to the shore, and the gander landed in the water near the sand bar.

The gander, honking infrequently, swam toward shore, but when he reached a point about 20 yards from the goose she honked and the gander returned. This pattern was repeated three more times. On the fourth return, the gander landed a few feet from the goose. Within three minutes the pair entered the water and swam about 15 yards toward shore. Then they flew back over the island and landed about 50 yards offshore on the opposite side. Almost immediately, they flew back over the island and landed near the place they originally flew from. Then they swam to the sand bar and landed. This pattern was repeated four times, flying closer to the nest each time.

The last time the goose landed on the sand bar, she went to the nest and began to rearrange it. The gander swam to the point where he was originally observed. The total elapsed time from the goose leaving the nest until she returned was 1 hour and 20 minutes.

The single goose was smaller than either one of the pair. This size difference suggests that the single was a yearling, possibly raised by the pair. Although Sherwood (1967) found that only one day was required to drive yearlings away when a nesting territory was established, female yearlings had a tendency to remain in their natal areas. If the gander regarded the island itself as a nesting territory, the tolerance for the single while the pair was off the island might be partially explained. Also, Brakhage (1965) found that although ganders were purposeful in defending their territories against other breeding geese, they were relatively tolerant of nonbreeding individuals. All of the interactions observed near nests involved lack of aggressive behavior, particularly ganders mated to incubating females. This behavior is interpreted as mostly atypical, possibly reflecting marginal nesting habitat.

Brood Grouping and Mixing. Brood aggregations have been reported by Culbertson *et al.* (1971) on a rearing area near Penawawa, with broods of 12, 18, and 20 tended by only two adults. When both marked and unmarked goslings were present, these investigators noted that brood grouping and exchange were common. Brood grouping in *Branta canadensis moffitti* has also been reported by Naylor and Hunt (1954), Geis (1956), and Hanson and Browning (1959).

On May 15, 1970, a group of seven adults and five goslings was observed on the mainland south of New York Bar Island. This group ran inland when the boat approached. A nearby pair of adults had 11 goslings of three distinct sizes—two appeared to be about three weeks old, eight were about one week old, and one was only a few days old. A steep bank forced the goslings into the water where they scattered. Although three other family groups were in the immediate area, within 15 minutes the scattered individuals reformed into their original family group.

A group of 15 goslings attended by only one adult was observed near Penawawa on May 16, 1970. No other geese were observed nearby.

Although the extent of such brood aggregations is unknown, Hanson (1956) believed they are uncommon in most areas. He stated that the "strength of the bonds between the young themselves" is as important as parent hostility to stray goslings in maintaining family groups. Collias and Jahn (1959) reported that goslings over about a week old will attack strange goslings, particularly when a size difference exists.

Brakhage (1965) stated that gang broods were probably a result of crowded rearing areas. Thus where nesting density is low and families do not normally contact other families until family bonds are established, brood aggregations should not occur.

The above viewpoints are not supported by observations made on the family group seen May 15 with 11 goslings. Two of these goslings were about two weeks older than nine others in the same brood. Since there was only one brood-rearing area in Unit A before inundation occurred, a crowded rearing area may account for the brood aggregations reported by Culbertson *et al.* (1971), even though nesting density in Unit A was low. The family group of one adult and 15 goslings observed on May 16, 1970, however, occurred when numerous rearing areas were available in Unit A. Either the published explanations for such behavior are inadequate for rationalization of the observed aggregations, or the observed behavior on the Snake River may have been atypical as a consequence of inundation.

Artificial Nesting Structures

Before the Snake River in southeast Washington was transformed from a free-flowing stream to a series of impoundments, there was no need for artificial nesting sites for geese. However, early surveys (Yocom, 1951; Buss and Wing, 1966), that showed geese using islands, cliffs, and shorelines for nesting and rearing their young, clearly indicated that many of these sites would be inundated or destroyed by the series of impoundments planned for this section of the river. At present, three of the four dams proposed for the lower Snake River have been completed. With the completion of Lower Granite Dam, at least 22 nesting islands will have been lost by inundation. Consequently, an experiment on the use of artificial goose-nesting structures was initiated in 1969 along the free-flowing stretch of river in Unit D and on Lower Monumental Reservoir in Unit C. Hopefully, these structures and some of the remaining cliff areas would be accepted for nesting purposes by at least some of the displaced geese.

No nesting occurred on the artificial structures during 1969. Placement of the structures was not completed until the nesting season was underway. On Lower Monumental Reservoir, the water level was raised after nesting activity had begun. In June, 1969, only two groups of goslings were found on the reservoir. Excessive disturbance, similar to that described above for Unit A, occurred along much of the free-flowing river where structures were installed.

In 1970 a completed nest was found in a structure during the nesting season. This structure is located on a sandy hill about 50 feet high and about 20 yards inland from the shoreline. Visibility is excellent in all directions. The nesting material was dried grass gathered at the site. All five eggs hatched.

A nest pit occurred in a structure located several yards from water at the head of a flooded draw. Steep slopes begin several feet from the base of the structure. A sheep, dead from unknown causes and lying against one leg of the structure, might have caused desertion.

A structure, refurnished on February 20, 1970, is located on a length of river where few geese were observed. A pair of geese was seen one-fourth to a half mile above this structure on several occasions during late February and the first half of March. Although no geese were seen from one mile above to a half mile below the structure after mid-March, a single goose was frequently observed about a half mile

below the structure. On March 31 the drum was checked by mirror. The nesting material appeared undisturbed, with no evidence of goose down or a pit, and no geese were seen in the general area. On April 4 a nest survey was conducted, and as the survey boat approached a goose was seen leaving the structure. Initial observation of the drum revealed no indication of nesting. Closer inspection of the layer of nesting material, however, revealed several lumps that proved to be five eggs in a well-constructed nest buried under several inches of material.

Published opinions concerning the most effective type of goose-nesting structure vary widely. Structures proposed and constructed have ranged from floating platforms supporting nest boxes to leg-supported platforms and nest structures placed in trees. Obviously, the type of structure utilized is somewhat limited by terrain and vegetation. Important considerations in design include relatively low cost, ease of construction, assembly, erection, maintenance, and acceptability by geese.

Rienecker (1971) studied six types of nesting structures and evaluated them with regard to the criteria listed above. One type was a split-drum structure similar to the design utilized in the present study. Rienecker (1971) concluded that "the split-drum is the most promising with regard to acceptance by the geese, low cost, stability, hauling, and assembly in the field."

Nesting structures have been available to the geese for one partial and one complete nesting season. For 1969, with the platforms available for only part of the season, 0 percent (0 out of 37) of the structures was used. For 1970, 6 percent (2 out of 35) of the structure were used.

In 1954 Craighead and Stockstad (1961) installed 83 platforms in the Flathead Valley in Montana. Over a five-year period an average of 73 platforms per year was available to the geese. Use of these platforms was approximately 2 percent (3 out of 73), 4.5 percent (6 out of 73), 8 percent (11 out of 73), and 9.5 percent (13 out of 73 for 2 yrs.) for 1954, 1955, 1956, 1957, and 1958, respectively.

Rienecker (1971) in California had nesting percentages of 15 (10 out of 65 platforms), 35 (24 out of 68 platforms), 44 (34 out of 78 platforms), and 53 (36 out of 68 platforms) for 1967, 1968, 1969, and 1970, respectively.

Such a pattern of gradually increasing usage is typical in the literature. The use of artificial structures by geese is probably influenced by both social facilitation (Crawford, 1939) and learning (Thorpe, 1951). In an area with no previous history of successful use of artificial structures, success or failure should be measured over a period of three to five years or more.

Summary and Conclusions

Counts of geese made in the study area from the last week in February through mid-May for 1965, 1967, 1968, 1969, and 1970 averaged 157, 97, 83, 90, and 89, respectively, per trip. Correspondingly, the number of island nests observed was 30, 27, 20, 10, and 1. Thus the average number of geese seen during 1968, 1969, and 1970 remained practically the same, but the proportion of geese nesting on islands declined conspicuously during these three years of major disturbances and reservoir impoundment.

Ten nests found in 1969 and three (2 nonisland nests) found in 1970 are the lowest numbers recorded since the study began in 1954. The long time spent searching for two nonisland nests, the extensive area searched, the very low maximum number

(23) of goslings seen on the study area in 1970, and the low percentage (probably representing only one brood) of goslings not accountable to a known nest support the conclusion that very few geese nested in the area during 1970 and attest to insignificant production of geese from nonisland nests. Excessive human disturbance and inundation of islands previously used for nesting almost certainly caused the drastic reduction in nesting.

A relatively high nesting success during years with relatively few nests suggests a density-dependent mechanism of controlling population numbers. In all ways, data on nesting collected in 1969-1970 supported those reported for 1954-1965 and 1966-1968 by Buss and Wing (1966) and Culbertson *et al.* (1971).

Observations on movements of marked geese obtained in 1969-1970, like those reported by Culbertson *et al.* (1971) and Hansen and Oliver (1951), suggest that the great basin Canada goose is a permanent resident in south-central Washington; at least part of the population winters within 50 to 100 miles of the study area.

Reactions of geese to reservoir impoundment were forcefully expressed by their unsuccessful attempts to establish territories. Their failure, which is attributed to partial or complete flooding of potential territories, is the key to unsuccessful nesting in the study area during 1970. Behavioral information on interactions near nests revealed a conspicuous lack of aggressive behavior, possibly reflecting marginal nesting habitat. Observations on brood grouping and mixing, collected in 1970, showed greater age differences among goslings of the same brood than those reported by other investigators. These observations may reflect atypical behavior as a result of habitat inundation during and preceding the brood rearing season.

Of 37 artificial nesting structures erected on shore of a reservoir and a stretch of free-flowing river in 1969, none were used that year. In 1970, however, when 35 of the original structures remained, two clutches and a nest pit (beginning of a nest) were found in these structures.

Acknowledgments

Acknowledgment is made to the U.S. Corps of Engineers for construction of the artificial nesting structures and transporting them to their field sites. The selection of sites for these structures was determined jointly by representatives of the Bureau of Sport Fisheries and Wildlife, the Corps of Engineers, the Washington Department of Game, and Washington State University during February and March 1969. This study was supported by the State of Washington Water Research Center and the U.S. Department of the Interior, Office of Water Resources Research, as authorized under the Water Resources Research Act of 1964. We appreciate the help provided by Washington State University students in wildlife biology who assisted with the collection of data, and the helpful suggestions made by Don E. Miller, Department of Zoology, Washington State University, and Frank M. Kozlik, California Department of Fish and Game, for improving the manuscript.

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Bacula of Two Western Moles

Bacula have not been described in North American moles, genus *Scapanus*. They have probably been overlooked due to their small size and their extreme distal position within the glans (Fig. 1). The purpose of this paper is to describe bacula from the Townsend mole, *Scapanus townsendi* (Bachman), the coast mole, *Scapanus orarius* True, and to compare these with the baculum of the European mole, *Talpa europaea* L., described by Didier (1951, Etude systematique de l'os penien des mammiferes. Mammalia 15:11-22).

The bacula of both *S. townsendi* and *S. orarius* are considerably smaller in all respects than that of *T. europaea* (Table 1). The baculum of *T. europaea* has a relatively straight surface and a swollen proximal end which tapers toward the distal end. Dorsally, the bone of *T. europaea* curves slightly to the right; the proximal end has a "V"-shaped protuberance. The lateral surfaces are slightly hollowed; the venter is flat with an irregular surface. The distal extremity tapers and ends in a very small, rounded tip. The bone is relatively smooth except for the granulated proximal end (Didier, *op. cit.*).

There is much overlap in size of bacula between the two species of *Scapanus*. However, the bacula of six *S. townsendi* have an average length of 0.42 mm and an average width of 0.27 mm, while those of five *S. orarius* have an average length of 0.48 mm and an average width of 0.22 mm. The bone of *S. townsendi* has an average (width to length) ratio of 1:1.63 and that of *S. orarius* has an average ratio of 1:2.30; the bone of *T. europaea* has a ratio of 1:3.50 (data from Table 1).

Bacula of *S. townsendi* and *S. orarius* are relatively transparent and not uniform in size or shape between individuals of the same species. Therefore, it is doubtful that these bacula are taxonomically significant on an individual basis.

Material Examined

Scapanus townsendi—10 mi. W Junction City, Lane Co., Ore., #CM 1918, 1934, 1973; 11 mi. W Junction City, Lane Co., Ore., #CM 2112; 1¾ mi. S Bandon, Coos Co., Ore., #CM 2272; 1 mi. SE Key Center, Pierce Co., Wash., #MLJ 5213; *Scapanus orarius*—10 mi. W Junction City, Lane Co., Ore., #CM 1898; 1¾ mi. E Bandon, Coos Co., Ore., #CM 2307; 4 mi. SE Bandon, Coos Co., Ore., #CM 2414; 10 mi E Brookings, Curry Co., Ore., #CM 2469; 1 mi. SE Key Center, Pierce Co., Wash., #MLJ 5214. All specimens are in the Puget Sound Museum of Natural History.

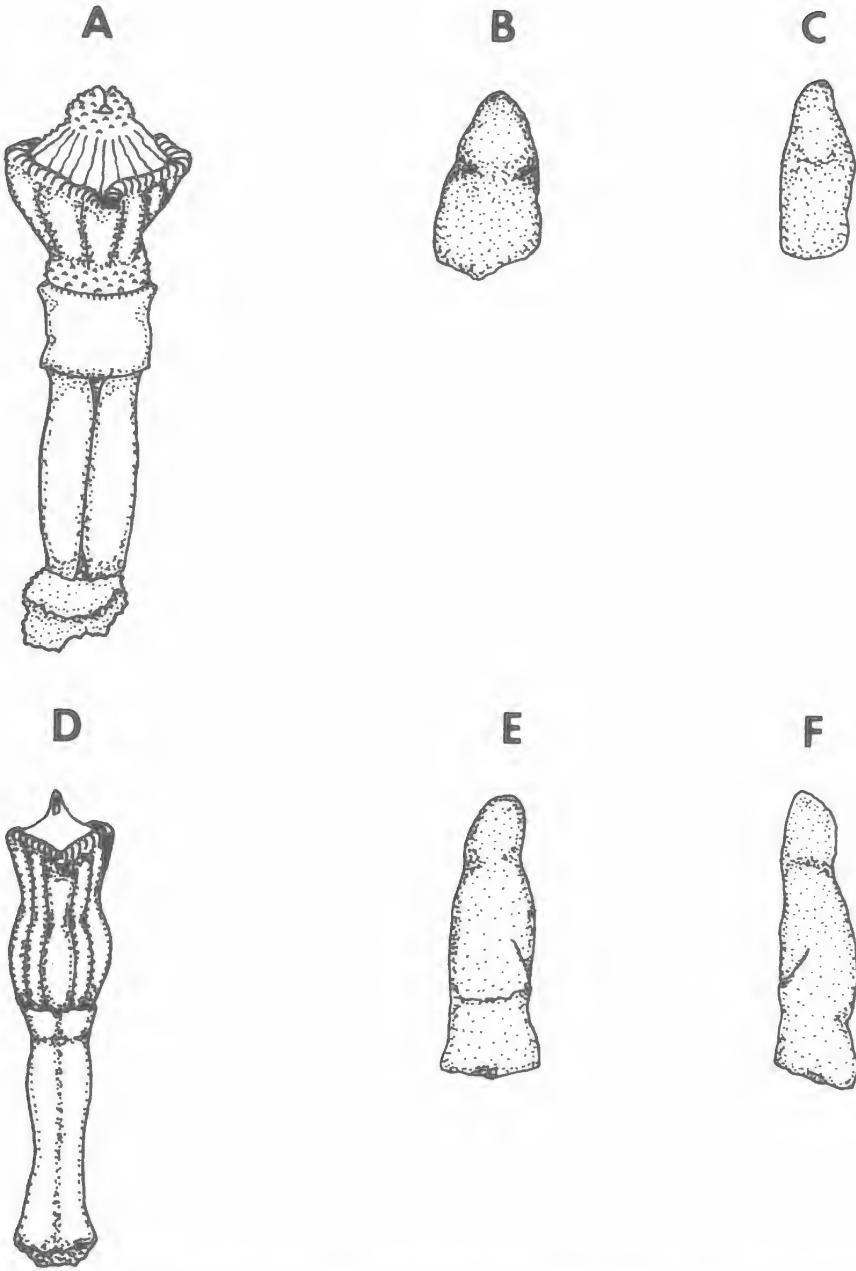


Figure 1. Penis and baculum of *Scapanus townsendi* and *Scapanus orarius*. A, penis of *S. townsendi*, CM 1934, X5.1; B, baculum of *S. townsendi*, CM 2112, X77, dorsal view; C, baculum, CM 2112, X77, lateral view; D, penis of *S. orarius*, CM 2469, X4.3; E, baculum of *S. orarius*, CM 2307, X85, dorsal view; F, baculum, CM 2307, X85, lateral view.

TABLE 1. Measurements of bacula from adult moles.

Catalog Number	Species	Greatest Length in mm	Greatest Width in mm
—	<i>Talpa europaea</i>	3.50	1.00
	<i>Scapanus townsendi</i>		
CM 1918*		0.36	0.28
1934		0.38	0.23
1973		0.44	0.18
2112		0.36	0.19
2272		0.59	0.42
MLJ 5213**		0.38	0.34
	<i>Scapanus orarius</i>		
CM 1898		0.32	0.20
2307		0.47	0.16
2414		0.58	0.25
2469		0.52	0.34
MLJ 5214		0.53	0.17

*CM=Chris Maser.

**MLJ=Murray L. Johnson.

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Tolerance of Lodgepole and Ponderosa Pine Seeds and Seedlings to High Water Tables

Introduction

Reasons for the distinct type lines which often occur between lodgepole and ponderosa pine stands in south-central Oregon are not clearly understood. Stands of almost pure lodgepole pine on depressions and flat areas with ponderosa pine or a mixture of ponderosa and lodgepole pine on adjacent higher sloping topography may be due to greater low-temperature tolerance of lodgepole seedlings during the emergence period (Berntsen, 1967). However, some of these lodgepole stands exist on areas with seasonal or permanent high water tables and, as summarized by Tarrant (1953), a number of investigations have suggested that lodgepole pine is more tolerant of high soil water levels than is ponderosa pine. The purpose of this study was to determine effects of high soil water levels on seed germination, seedling survival, and early growth of lodgepole and ponderosa pine.

Methods and Materials

Apparatus

To control soil water contents in the suction range between 0 and -50 cm of water, the apparatus shown in Figure 1 was constructed. An Alundum filter disk was cemented with PVC cement 5 cm from the bottom of a Lucite cylinder 17 cm in length and 10 cm in diameter. A Lucite plate was then fastened to the bottom of the cylinder, and two Lucite tubes 3 cm long were fastened in holes drilled through the cylinder wall 1 and 4.5 cm from the Lucite plate. The lower tube was used as a water inlet, and the upper tube was used to remove air bubbles from beneath the filter disk.

The small pores in the filter disk allow the disk to support a hanging water column. Height of the hanging water column above free water level in the jug controls soil pore sizes which will take up water through the wet porous disk. At equilibrium, there is a water gradient in the soil corresponding to a suction gradient of 1 cm of water per cm depth of soil.

Soils

Soil materials used in this study were taken from the A1 horizon of a Lapine soil, the AC horizon of a Wickiup soil, and from the upper foot of a small peat bog. The Lapine soil is a well-drained benchmark series developed on Mazama pumice. Reservoir construction in recent years has subjected small acreages of this soil which support both lodgepole and ponderosa pine to periodic flooding. The Wickiup soil is the most common poorly drained soil developed on Mazama pumice in south-central Oregon. Wickiup soils support stands of lodgepole pine with very little, if any, ponderosa.

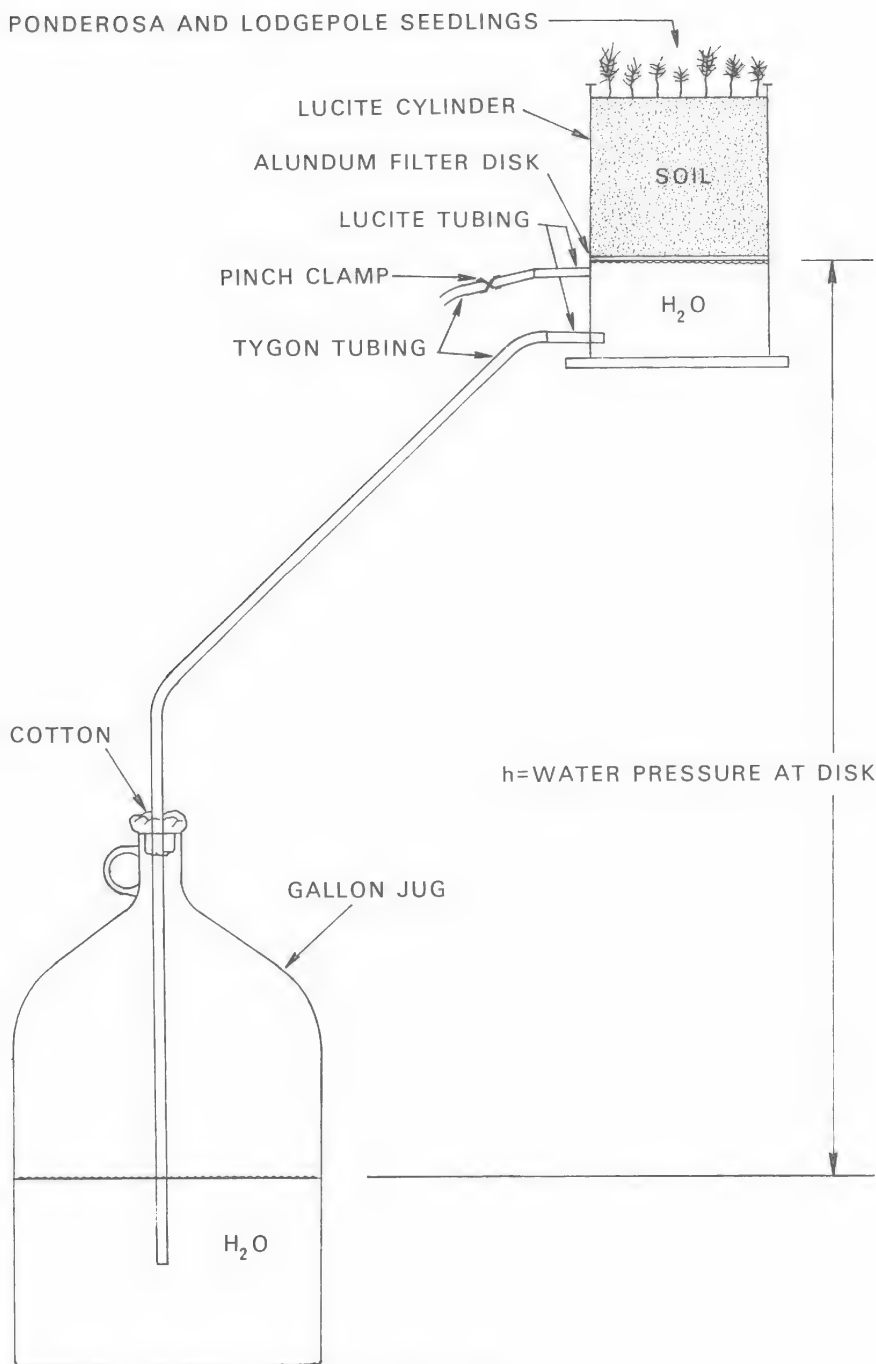


Figure 1. Apparatus for controlling soil water suction.

The peat bog occupies a topographic depression and has a water table within 10 cm of the soil surface. Although the bog is surrounded by Lapine soil supporting a mixed stand of lodgepole and ponderosa pine, only a few small lodgepole saplings are present on the peat soil.

Seeds

Seeds used in all experiments were collected at an elevation of 4500 ft approximately seven miles west of Lapine, Oregon. Germination of the lodgepole seed lot was 84 percent, compared with 72 percent for the ponderosa seed lot.

Experimental Design

Five different experiments were run using the cylinders. All experiments were completely randomized split-plot designs. In experiments 1-4, soil water level was the whole plot treatment and species was the sub-plot treatment. In experiment 5, length of time that the water level was maintained at the surface was the whole plot treatment.

Germination

Methods

The first experiment tested the hypothesis that high soil water level did not affect germination of either species. Soil material from the Wickiup AC horizon was put through a 2 mm sieve. This material was packed in the cylinders at a density of 0.72 g/cm³. Soil depth was 5 cm. Ten seeds of lodgepole and 10 seeds of ponderosa pine were planted in each cylinder so that their tops were level with the soil surface. The free water levels were then adjusted so that water pressures at the upper soil surface equivalent to 0, -5, -10, -15, and -20 cm of water were obtained in the different cylinders. Each treatment was replicated four times. Percent germination values were angularly transformed (Li, 1957) before subsection to analysis of variance.

Results

Greater total numbers of lodgepole seed germinated because of the higher percent germination of the lodgepole pine seed lot. As free water rose from 15 to 5 cm of the soil surface, ponderosa seed germination was limited more than lodgepole (Fig. 2 and Table 1). Some germination for both species occurred on saturated soil, but the number of germinants was very small.

TABLE 1. F values for split plot analysis of the measured variables for experiments 1 through 4.

Variable	Soil	Soil water pressure	Species	Species x soil water pressure
Germination	Wickiup AC	18.13*	24.93*	3.27*
Seedling dry weights	Lapine A1	2.69	649.92*	2.61
	Peat	2.73	184.54*	4.35*
	Wickiup AC	12.03*	538.79*	2.22
Top-root ratios	Lapine A1	0.20	1.85	0.09
	Peat	1.40	.81	2.01
	Wickiup AC	9.25*	1.21	7.96*

* Significant at the 5 percent probability level.

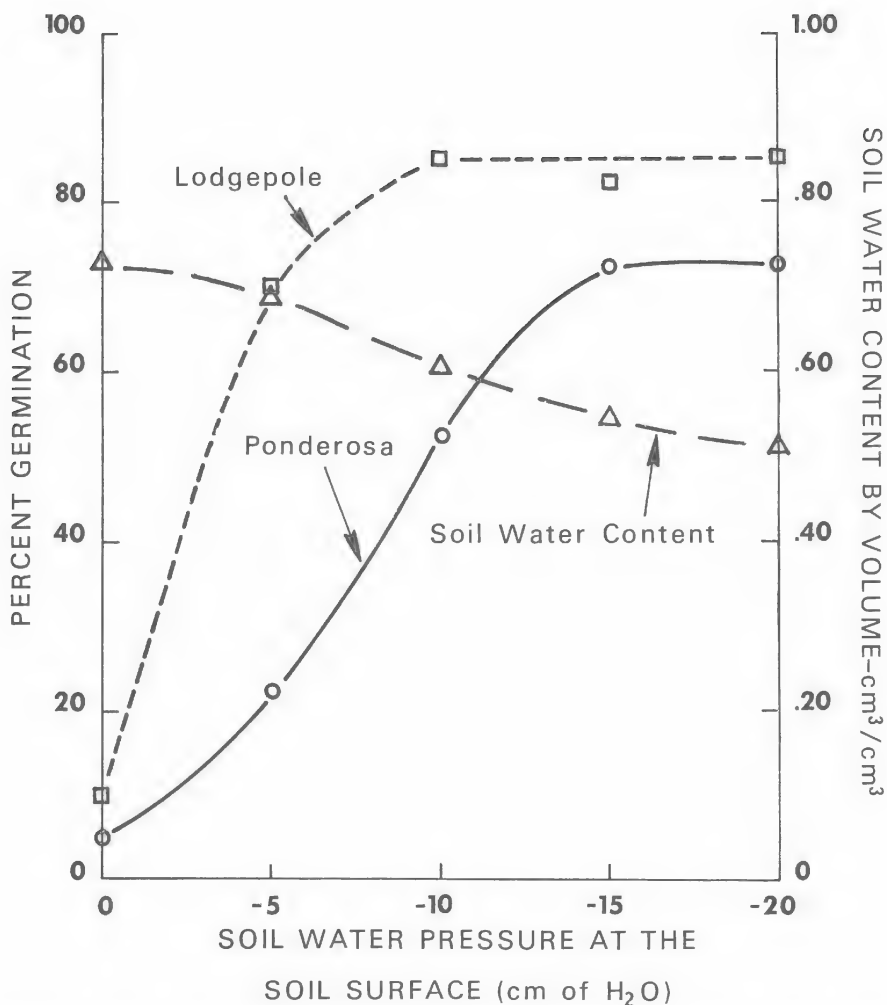


Figure 2. Percent germination of lodgepole and ponderosa pine seeds and soil water content by volume as a function of water pressure at the soil surface. Each point represents an average of four replications.

Survival and Growth—Soil Water Level

The second, third, and fourth experiments tested the hypothesis that high soil water level has no detrimental influence on survival or growth of either species.

Methods

In the second experiment, seedlings were germinated in perlite; and when one week old, four seedlings of each species were transplanted to soil in each individual Lucite cylinder. The soil was Lapine A1 horizon material packed at a density of 0.70 g/cm³. Soil depth was 10 cm. Before transplanting of seedlings, water levels were adjusted

so that water pressure was equivalent to -40 cm of water at each disk. One week after transplanting of seedlings, free water levels were changed so that pressures at various disks were equivalent to +10, +5, 0, -5, -10, -20, -30, and -40 cm of water. Each water pressure was replicated twice.

In the third experiment, the procedure of the second experiment was followed except a peat soil was used. The peat was put through a 2 mm sieve and packed into cylinders at a bulk density of 0.30 g/cm³.

The fourth experiment was similar to the second and third experiments, except only four different pressures were applied at the disk surfaces (+10, 0, -10, and -20 cm of water equivalents) and each pressure was replicated four times. The soil used was Wickiup AC horizon put through a 2 mm sieve and packed to a bulk density of 0.72 g/cm³.

For all three experiments, seedlings were allowed to grow in a greenhouse for 130 days, the length of time necessary for the majority of trees of both species to set buds. The greenhouse photoperiod was 15 hours, and average day and night temperatures were approximately 78° and 65° F. Oxygen diffusion rate was then measured as described by Letey and Stolzy (1964). Five platinum microelectrodes were placed with tips at 1.5-, 5-, and 9.5-cm depth within the soil in each cylinder for a total of 15 measurements within each cylinder. After determination of soil oxygen diffusion rates (ODR's), the plants were removed and soil water content, oven-dry weights of tops and roots, and top-root ratios for the plants were determined.

Results

In experiment 2, where seedlings were transplanted into Lapine A1 horizon material, no mortality occurred even under saturated conditions. Although dry seedling weights tended to be lower for plants grown under saturated conditions, the lower weight was not significant (Tables 1 and 3). Weights of ponderosa seedlings were significantly greater than weights of lodgepole seedlings, but this is to be expected since dry weight of a week-old ponderosa pine seedling is approximately four times that of lodgepole. Species differences in weight were not influenced by soil water levels. The ODR's for this experiment ranged from 0.061×10^{-6} g O₂/cm²-min for saturated soils up to 0.191×10^{-6} g O₂/cm²-min for the driest A1 soils (Fig. 3). These values represent averages of 15 measurements and they indicate that even the driest soil was poorly aerated. There was only a 13 percent difference in volumetric water content between the wettest and driest treatments (Table 5).

Top-root ratios averaged 1.7 for ponderosa pine and 1.5 for lodgepole pine (Table

TABLE 2. F values for split plot analysis of seedling dry weights and top-root ratios for experiment 5.

Variable	Soil	Weeks of soil saturation	Species	Species x weeks of soil saturation
Seedling dry weights	Wickiup	2.13	42.51*	0.17
Top-root ratios	—	2.02	11.87*	4.59*

* Significant at the 5 percent probability level.

3). This difference was not significant, and top-root ratios were not influenced by soil water pressures (Table 1).

For experiment 3 where peat soil was used, survival of both species was again excellent. A total of four lodgepole pine and two ponderosa pine were lost, none

TABLE 3. Average dry weights of individual seedlings as a function of soil water pressure.

Species	Water pressure	Dry weights			Top-root ratios		
		Lapine A1	Peat	Wickiup AC	Lapine A1	Peat	Wickiup AC
	<i>cm of H₂O</i>	<i>g</i>					
Ponderosa pine	+10	0.11	0.12	0.08	1.2	1.7	1.6
	+ 5	.18	.38	----	1.5	1.4	---
	0	.17	.33	.09	1.8	2.4	1.2
	- 5	.16	.41	----	1.7	1.8	---
	- 10	.19	.56	.10	1.9	1.9	1.0
	- 20	.17	.44	.11	1.8	2.0	.9
	- 30	.17	.45	----	1.5	2.0	---
	- 40	.15	.43	----	2.0	1.8	---
Average		0.16	0.39	0.10	1.7	1.9	1.2
Lodgepole pine	+10	0.04	0.06	0.02	1.0	1.5	1.2
	+ 5	.05	.12	----	1.2	1.7	---
	0	.05	.12	.05	1.2	1.8	1.2
	- 5	.05	.22	----	1.1	1.7	---
	- 10	.04	.12	.04	2.4	2.2	1.0
	- 20	.06	.13	.03	1.8	2.2	1.0
	- 30	.06	.09	----	1.5	2.2	---
	- 40	.05	.13	----	1.8	1.8	---
Average		0.05	0.12	0.04	1.5	1.9	1.1

TABLE 4. Oxygen diffusion rates (ODR) and average dry weight and top-root ratios of individual lodgepole and ponderosa pine seedlings as a function of length of soil saturation.

Length of soil saturation	ODR x 10 ⁻⁶	Dry weight		Top-root ratio	
		Ponderosa pine	Lodgepole pine	Ponderosa pine	Lodgepole pine
weeks	<i>g O₂/cm².min</i>	<i>g</i>			
52	0.05	0.38	0.18	0.57	0.58
21	.42	.32	.14	.62	.80
12	.40	.42	.20	.67	.87

TABLE 5. Average soil water content by volume as a function of water pressure at the disk for experiments 2, 3, and 4.

Water pressure at disk	Lapine A1	Soil water content	
		Peat	Wickiup AC
<i>cm of H₂O</i>		<i>cm³/cm³</i>	
+10	0.62	0.95	0.73
+ 5	.57	.90	----
0	.59	.85	.64
- 5	.55	.86	----
- 10	.53	.86	.52
- 20	.51	.72	.48
- 30	.51	.68	----
- 40	.49	.70	----

in saturated soil. Again, seedlings produced under saturated conditions tended to be smaller, but this tendency was not significant. Ponderosa pine seedlings were again significantly larger than lodgepole, and this difference was influenced by soil water level

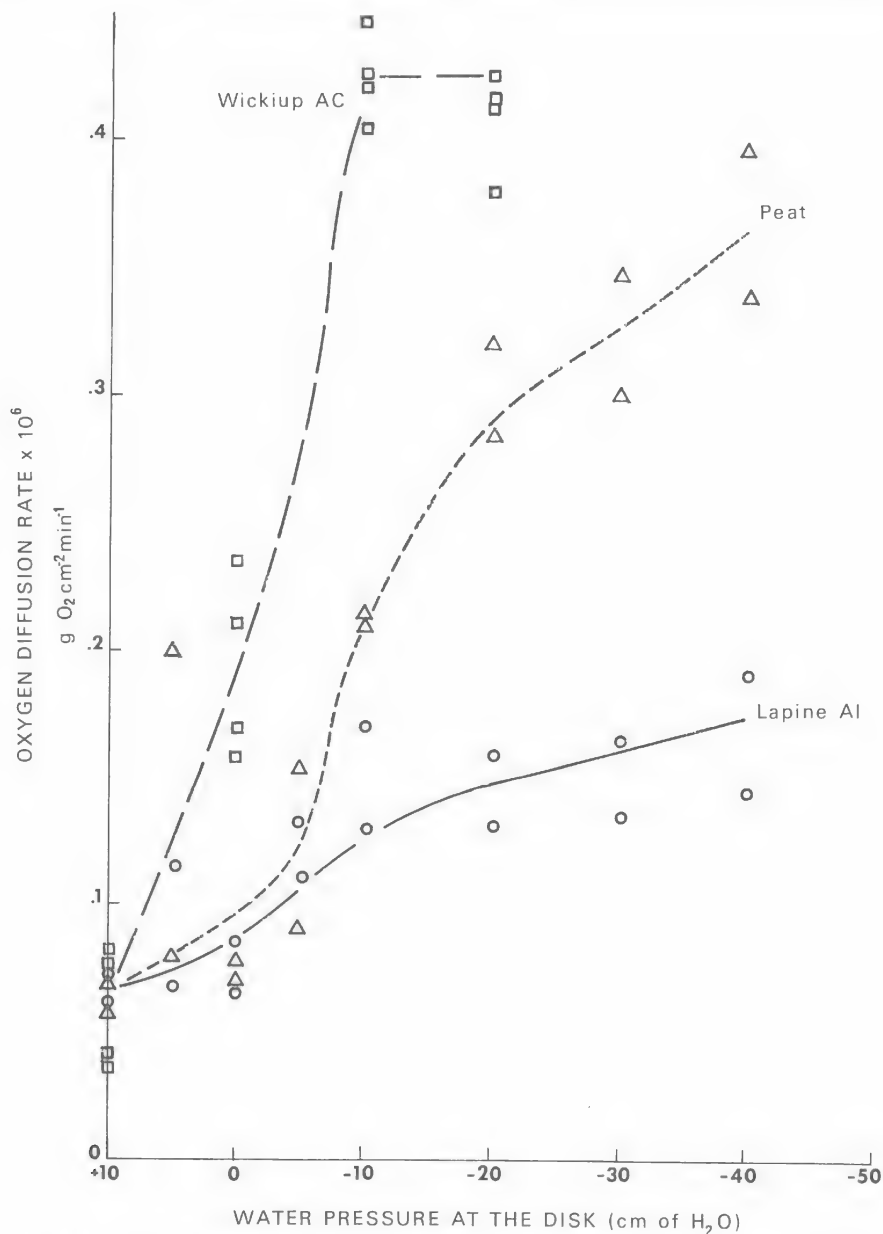


Figure 3. Oxygen diffusion rates as a function of water pressure at the disk. Each point represents an average of the 15 measurements taken in each cylinder.

(Tables 1 and 3). Oxygen diffusion rates ranged from 0.061×10^{-6} g O₂/cm²-min to 0.399×10^{-6} g O₂/cm²-min, indicating greater soil aeration than in the Lapine A1 horizon (Fig. 3). This soil also exhibited a greater range of soil water content than the Lapine (Table 5). Under these conditions, decreasing soil water pressure coupled with decreasing soil water content and increasing soil aeration seems to favor growth of ponderosa pine over that of lodgepole pine. Top-root ratios did not change significantly for either species as soil water levels changed (Table 1). Average top-root ratios were 1.9 for both species (Table 3).

In experiment 4, with poorly drained Wickiup soil, survival of both species was again excellent. Only one seedling of each species was lost, and these losses took place in the driest soil. Oxygen diffusion rates were more widely spread— 0.038×10^{-6} g O₂/cm²-min to 0.448×10^{-6} g O₂/cm²-min—than in the Lapine A1 and peat soils (Fig. 3). Again, ponderosa pine seedlings were bigger than lodgepole pine (Tables 1 and 3). Both species increased in size where water contents were lowered before saturation. Increasing depth to free water and the accompanying increase in aeration did not favor growth of ponderosa pine over lodgepole pine as was the case with peat soil.

Top-root ratios decreased more for ponderosa pine with decreasing soil water levels than for lodgepole pine (Tables 1 and 3).

Methods

The fifth experiment tested the hypothesis that the length of time soil is saturated affects growth and survival of both species identically. Four one-week-old ponderosa and four one-week-old lodgepole seedlings were transplanted into cylinders containing soil from the Wickiup AC horizon. The soil was put through a 2 mm sieve and packed to a density of 0.72 g/cm³. Soil depth was 5 cm.

For two weeks after transplanting, a pressure equivalent to -30 cm of water was applied to the disk surfaces. Then the free water level was adjusted so that pressure was equivalent to +5 cm at the disk surfaces. This saturated condition was then maintained for 12 weeks in four cylinders, 21 weeks in four other cylinders, and 52 weeks in four additional cylinders. In the 12- and 21-week treatments, pressure was lowered to the original -30 cm of water at the disk surface after the saturated period was over. The plants in the 12- and 21-week treatments were then allowed to grow at original soil water pressure for the remainder of the year, when the entire experiment was terminated. Oxygen diffusion rates were measured at depths of 1.5 and 4.5 cm. Five determinations were made at each depth for a total of 10 measurements per cell. Plants were then removed, and the oven-dry weights and top-root ratios were determined.

Results

Survival of both species was good. In all but two cylinders, at least three plants of each species survived. In one of the cylinders where soil was saturated for 52 weeks, only two lodgepole pine survived; and in one other cylinder where soil was flooded for 12 weeks, only one lodgepole pine survived. Treatment did not significantly influence survival, and there was no significant difference in survival between species.

Total dry weights were not influenced by length of time that the soils were saturated (Tables 2 and 4). Ponderosa pine was heavier than lodgepole pine, but this is to be expected because of its initially larger size.

Top-root ratios of lodgepole pine were larger than top-root ratios of ponderosa for treatments flooded 12 and 21 weeks (Tables 2 and 4).

The majority of plants of both species set buds during the twelfth week of flooding. Reducing water pressure at the plate surface provided a more favorable ODR (Table 4). Still, neither species responded by significantly increasing total dry weights.

Root Morphology

In all of the experiments where plants were grown until bud-set, a modification of root development was noted for both species in saturated and near-saturated treatments (water pressures equivalent to +10, +5, and 0 cm of water at the disk surface). Root depth and the number of lateral roots were restricted, and the roots exhibited a radial swelling. Root cross sections revealed a normal center protosteles. However, the pericycle was enlarged somewhat more than normal, and both cells and intercellular spaces were large. Greatest deviation from normal was in the cork cambium which did not produce regular periderm cells. Instead, the cork cambium intermittently formed ridges of suberized parenchyma with very large cells and intercellular spaces. Such root development is usual in flood plant tissue.

Discussion and Conclusions

Seeds and seedlings of both species exhibited a surprisingly high tolerance to very wet soils and low oxygen diffusion rates.

The differences in germination of the two species with soil water level coupled with more frequent lodgepole pine seed crops may be a factor governing the presence of lodgepole pine on some sites. Areas do exist where water tables are within 15 cm of the surface during the germination period, and the extent of these areas varies from year to year. However, it is safe to say that the total extent of these areas is not great compared with the total lodgepole acreage even in the wettest springs. Extensive areas of lodgepole on soils where water tables are deeper than 15 cm or absent suggest other environmental factors influence stand distribution patterns.

High soil water levels, including saturation, did not cause significant mortality of either species even when the saturation period was 52 weeks. This result is particularly interesting for ponderosa pine which normally but not always grows on well-drained sites throughout its range. This high tolerance of saturated conditions may change with age for one or both species. However, exclusive presence of lodgepole pine on soils with high water tables is not a result of differential species tolerance to high soil water content alone during the early seedling stage.

Growth of both species combined tended to be lower on the saturated treatment for both Lapine A1 horizon and peat soils. Perhaps these differences would have been significant if more replications had been employed. Growth of both species combined was significantly decreased by raising water levels for the Wickiup soil where more replications were used. Growth of the two species was influenced differently by changing soil water levels only for peat soil. For peat, decreasing soil water levels produced greater increases in ponderosa than in lodgepole pine growth. Perhaps exclusive presence of lodgepole in the peat bog is because lodgepole seedlings are able to grow better than ponderosa seedlings under the very wet conditions. Lodgepole may be able eventually to grow above the 18 inches of grass and forb competition, but ponderosa pine may never grow well enough to do so. Since no differences in species

dry weights occurred with changes in soil water level for the mineral soils, differences in growth rates in the early seedling stage cannot explain the exclusive presence of lodgepole on mineral soils with high water tables.

Significant differences in top-root ratios were obtained only in experiments where Wickiup AC horizon soil material was used. Top-root ratios of ponderosa pine decreased more with decreasing water levels than those of lodgepole. This is contrary to what would be expected if lodgepole root growth is more tolerant to high water levels and low soil aeration. The larger top-root ratios for lodgepole in experiment 5 for plants flooded for 12 and 21 weeks indicate that lodgepole had no more and perhaps even less ability to increase its root system after initial flooding than did ponderosa. The lack of change in dry weights with treatment in experiment 5 indicates that initial flooding prevents both species from immediately responding to lowered water levels.

Stolzy and Letey (1964) report that root growth of snapdragons was reduced or stopped when soil ODR's were in the range of 0.18 to 0.23×10^{-6} g O₂/cm²-min. Newport bluegrass required an ODR of 0.20×10^{-6} g O₂/cm²-min for root growth, and barley can grow roots at an ODR as low as 0.15 . The present study indicates that both lodgepole and ponderosa pine seedlings can tolerate much lower oxygen diffusion rates than these plants.

This study shows that for the seed source used the influence of high soil water content alone on initial survival and growth of both species is not a factor governing "wet-site" occupancy by lodgepole pine on mineral soils.

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Radiative Temperatures in the Willamette Valley¹

The stream of radiant energy incident upon the surface of the earth is absorbed, reflected, and transformed by myriad elements, each with differing thermal characteristics. The absorption of radiation is balanced effectively by the processes of convection, change in stored energy, latent-energy exchange, and emission of radiation. These dissipation processes are all temperature dependent, and the temperature of an exchanging surface adjusts to an equilibrium value that depends upon the relative effectiveness of the dissipation processes.

The equilibrium surface temperature of a landscape unit is related to the efficiency of that unit in absorbing and dissipating energy. Budyko (1958) discussed the temperature of natural surfaces and suggested that this may be a better parameter for use in bioclimatic studies than the degree-days that are accepted widely at present. Only recently have the means for such surface temperature measurements become generally available (Lenschow and Dutton, 1964).

We shall examine equilibrium temperatures attained by several different surfaces under intense solar irradiation that is characteristic of cloudless summer skies in the Willamette Valley. The observed values are a contribution to an inventory of surface temperatures of various landscapes; comparisons among the temperatures attained under these uniform conditions will contribute to a better understanding of the role of surface characteristics in the transformation of solar energy.

Field Experiments

The field experiment included a survey of surface temperatures with the aid of an infrared thermometer. The measurement conditions and techniques employed have a bearing on the interpretation of infrared temperatures.

Conditions of Measurement. Measurements reported here were made between 1230 and 1345 hours, PDT, on August 2, 1967, during a period of clear, dry weather. My measurements at the site of the Corvallis Agricultural Weather Station showed that the air temperatures within the instrument shelter changed slowly from 34°C at 1230 hours to 36°C at 1345 hours. Incoming solar radiation, measured with a Kipp pyranometer, was steady during the period of measurements. The initial value at 1230 hours was 1.22 cal cm⁻²min⁻¹, and subsequent values were: 1300, 1.24; 1315, 1.24; 1330, 1.22; and 1345, 1.21. Winds were light during the period of measurement.

Methods of Measurement. The surface temperature measurements were obtained with an infrared thermometer² that senses radiation emitted by the target surface in the wavelengths between 8 and 14 microns. The thermometer's field of view was 3 degrees, so the radius of the sampled area is about 1/40th of the distance between the instrument

¹ Paper 818, School of Forestry, Oregon State University, Corvallis, Oregon 97331.

² Barnes Engineering Company, Stamford, Connecticut 06902. Infrared Thermometer IT-3.

and the target. The resolution of the thermometer is given as 0.5°C , and its absolute accuracy is 2°C for a target above 0°C with an emissivity of unity. A battery-powered, frequency-controlled inverter³ provided 120 volts AC for mobile operation of the infrared thermometer.

A helicopter was used as an observation platform above the sampled surfaces. Observations were made between 60 and 100 m above the surface, though no height effects could be distinguished on temperatures measured from heights as great as 250 m.

Special Considerations in Infrared Thermometry. Several factors influence the accuracy obtained in infrared thermometry. These include transmissivity of the atmosphere, emissivity and reflectivity of the target surface, and instrument drift.

The influence of absorption and emission characteristics of the atmospheric gases between the instrument and the target is minimized by restricting the sensitivity of the instrument to the 8-14 micron band of the radiation spectrum. Lorenz (1966) reported that these effects could be neglected if the distance to the target did not exceed 100 m, providing measurement accuracies of $1-2^{\circ}\text{C}$ were acceptable.

The emissivity of the target surface also plays a role in the accuracy of the measurements. The most direct effect can be seen by differentiating the Stefan-Boltzmann Law

$$L_g = \epsilon \sigma T^4 (\text{cal cm}^{-2} \text{min}^{-1}) \quad (1)$$

where L_g is the emitted radiation flux density, ϵ is the emissivity, σ is the Stefan-Boltzmann constant, and T is absolute temperature to produce

$$dL_g/L_g = d\epsilon/\epsilon + 4dT/T \quad (2)$$

so that if a constant flux is received by the measuring instrument

$$d\epsilon/\epsilon = -4dT/T. \quad (3)$$

Thus at 298°K , an error of 1.0°C will be induced by a 1.3 percent error in the estimated target emissivity, unless the emissivity is compensated for by surface reflection. Because reflectivity of an opaque surface is equal to $(1 - \epsilon)$, the failure of the target to emit will be precisely compensated for if the flux of longwave radiation incident upon the target originated from a source at the same temperature as that of the target.

Two points are pertinent to our discussion of temperatures measured by infrared radiometry. First, the infrared thermometer is restricted to the 8-14 micron band of the longwave spectrum, and there is little emission by the atmosphere in the 8-14 micron region of the radiation spectrum. Consequently, under clear skies there is little compensation for the deviation of surface emissivity from unity (Lorenz, 1966), and equation (3) applies to our measurements. Strictly speaking, however, equation (3) is based on the entire spectrum and upon the assumption that the target surface emits as a gray body. Second, the emissivity of vegetative canopies is uniformly high, because of properties of the individual leaf elements and the "trapping" effect when leaves are assembled into a canopy. For example, recent reports (Fuchs and Tanner, 1966) give canopy values of 0.976 for sudangrass and 0.977 for alfalfa. The emissivity values for nonvegetated natural surfaces are not as precisely known, but generally range about 0.9. All temperatures reported in this paper are observed temperatures; appropriate corrections for emissivity would raise the figures slightly for water and vegetation, and perhaps substantially for soil and concrete.

³Terado Corporation, St. Paul, Minnesota 55108. Trav.-Electric Model 50-160.

Instrument drift may be eliminated conveniently with a simple blackbody. For a reference standard during the measurements, I used a water-filled, copper container equipped with an agitator, a suitable cone-shaped cavity, and a mercury thermometer.

Because of these factors, the readings obtained by the infrared thermometer may be within 2-3°C of the absolute value. The sampling problems encountered in measuring a mean surface temperature are not worked out, however. Therefore, the measurements reported here are best viewed in a relative sense.

Results and Discussion

Measured Values. Measurements reported here were obtained near Corvallis during the 1¼-hour period centered on solar noon August 2, 1967. The samples included a variety of the landscape features common to the central Willamette Valley. The data are presented in Table 1, ordered with respect to maximum temperatures. Data

TABLE 1. Midday temperatures of various surfaces. Infrared thermometer measurements made under cloudless skies in August 1967.

Surface	Range	Midpoint
	(°C)	
Ploughed fields	53-59	56
Urban Corvallis	46-57	52
Burned fields	46-56	51
Dried grass	40-45	42
Stubble fields	34-42	38
Clover fields	30-34	32
Coniferous forests	29-31	30
Deciduous forests	27-29	28
Irrigated corn	23-26	24
Willamette River	18-20	19

of this type, not conducive to statistical analysis, are presented merely in terms of the temperature range observed, with the midpoint of the range indicated for ease in making qualitative comparisons between surfaces.

In general, the variability within a particular surface was only 1-2°C; the wider ranges shown result from observations over several different sample units. Also, as one would expect, the surfaces with the higher temperatures showed greatest variation, both within and between sample units.

Relationship to the Surface Heat Budget. Solar radiation reaching a surface may be partly rejected by reflection, partly stored, partly dissipated by convection into the air, and partly utilized in the evaporation process. The efficiency of these transfer processes determines the equilibrium temperature of the exchanging surface. The processes are well understood for leaf elements (Knoerr and Gay, 1965, among others) and are now becoming better defined for vegetated surfaces (Gates, 1970).

The role of the transfer processes may be discussed with reference to the tabulated data in Table 1. The albedo, or reflected fraction of solar radiation, plays a direct role. Although albedos were not measured over these surfaces during the experiment, work here (unpublished) and elsewhere (Robinson, 1966, Chapter 6) allows the following albedos to be estimated with confidence: Willamette River, burned and ploughed fields, 7-10 percent; coniferous forest, 10-12 percent; deciduous forest, 15 percent; dry grass and stubble, 15-20 percent; and green crops, 20-22 percent. Note that the

coldest and the warmest surfaces have the lowest albedos. Apparently, efficiency in absorption need not correlate well with the surface temperature.

The availability of water for evaporation plays the major role in setting the equilibrium temperature level. For example, the irrigated corn was about 24°C, but an adjacent, nonirrigated cornfield was about 30°C. Also, the river was the coldest surface sampled, at 19°C. The large heat capacity of such a surface, however, contributes to a low temperature, despite a low albedo. The lack of water for evaporation at the surface of the ploughed and burned fields, combined with their low albedos and heat capacity, results in the high temperature levels observed there.

The forest stands also have low albedos, but they maintain low temperatures. Individual leaves in the open forest canopies are able to exchange energy effectively by convection as well as by evaporation. As noted elsewhere (Lorenz and Baumgartner, 1970), forest canopies seldom deviate far from air temperature. This finding holds in conifers even when water may not be freely available for evaporation.

Summary

An aerial survey of various surfaces was made with an infrared thermometer under cloudless skies. The temperatures reported can be compared readily because uniform weather conditions prevailed during the midday period of the measurements. The temperatures also may be referenced against a screen air temperature of about 35°C.

In general, vegetation remained near or somewhat below screen temperature, but nonvegetated surfaces rose considerably above. The differences are related to the relative efficiencies with which the surfaces partition absorbed solar radiation into reradiation, storage, convection, and evaporation. The availability of water for evaporation plays a major role in establishing the equilibrium temperature of a surface. Information on equilibrium temperatures contributes to a better understanding of the thermal response of irradiated natural surfaces.

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The Glacial Geomorphology of the Puget Lowland, Washington and British Columbia: Further Comments and References

The recent paper by Folsom (1970) was very useful in bringing together much of the relevant literature on the Pleistocene in the above area, and we wish to congratulate him. The following are references to works not included in Folsom's list, some of which he omitted while others have appeared since his paper. As a few items on his list refer to the mountain areas adjacent to the Puget Lowland in Washington, we have included some papers dealing with Pleistocene events in the south coastal mountains of British Columbia. We would point out, however, that two of Folsom's references (Fulton, 1968; Johnston, 1926) fall well outside the areal scope implied by his title, and that if the intent was to include all of Washington and British Columbia, many more works could be added.

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Contents

Number 1 (February)

Toys of Indian Children Bette E. Meyer	1
The Rocks and Structure of the White Pass Area, Washington Jack A. Ellingson	9
Habitat Improvement—The Way to Higher Wildlife Populations in Southeast Washington Richard J. Poelker and Irven O. Buss	25
Rhodophylloid Fungi of the Pacific Coast (United States) II: New or Interesting Sugeneric Taxa of <i>Nolanea</i> David L. Largent and Harry D. Thiers	32
Geographic Distribution of Micropezidae in the Western United States (Diptera) Richard W. Merritt	40
Plant Moisture Stress Patterns in <i>Eurotia lanata</i> and <i>Atriplex confertifolia</i> Lesley D. Love and Neil E. West	44
Effects of Aerial Forest Fertilization with Urea Pellets on Nitrogen Levels in a Mountain Stream K. W. Malueg, C. F. Powers, and D. F. Krawczyk	52
Vegetation and Soils of a 30-year Deer and Elk Exclosure in Central Washington A. R. Tiedemann and H. W. Berndt	59
Evaluating Forest Sites for Potential Growth Response of Trees to Fertilizer R. H. Waring and C. T. Youngberg	67
Association News	75

Number 2 (May)

Correlation of West Blacktail Ash with Pyroclastic Layer T from the 1800 A.D. Eruption of Mount St. Helens Rose Okazaki, Henry W. Smith, Raymond A. Gilkeson, and Jerry Franklin	77
The Microtool Industry of the Ice Mountain Microblade Phase Jason W. Smith and James Calder	90
National Park Wildlife Management Policy: A Case Study in Decentralized Decision-Making Daniel H. Henning	108
Trace Element Analyses of Columbia River Water and Phytoplankton C. E. Cushing and L. A. Rancitelli	115

A Bibliography of Oregon Ornithology (1935-1970), with a Cross-Referenced List of the Birds of Oregon J. Michael Scott, Thomas W. Haislip, Jr., and Margaret Thompson	122
Growth and Reproduction of Red Elderberry on Subalpine Rangeland in Utah Paul W. Conrad and Walter T. McDonough	140
Comparative Limnology and Phytoplankton Ecology of Four "Oligotrophic" Lakes in Oregon, U.S.A., with Emphasis on Lake Typology Douglas W. Larson	149

Number 3 (August)

Heavy Minerals, Pyroclastic Layers, and Alluvial Chronology: An Example Laurence R. Kittleman	165
Phosphorus and Algal Growth in the Spokane River Richard J. Condit	177
Experimental Infections with Fasciola hepatica from Eastern Washington and Northern California Bruce Z. Lang	190
Seasonal Variations in Forest Birds of Western Oregon Stanley H. Anderson	194
A Numerical Study of the Wing and Leg Muscles of Tinamous (Tinamidae) George E. Hudson, Donald O. Schreiweis, Sy Ying Chen Wang, and Douglas A. Lancaster	207

Number 4 (November)

A Species of the Genus Eunice (Polychaeta) from the Pacific Northwest Coast Rita M. Gustus	257
Fluctuations of Aquatic and Terrestrial Invertebrates in Drift Samples from Convict Creek, California Thomas M. Hinckley and Harry D. Kennedy	270
Comparative Food Habits of Four Species of Stream-Dwelling Vertebrates (Dicamptodon ensatus , D. copei , Cottus tenuis , Salmo gairdneri) Arthur L. Antonelli, Ronald A. Nussbaum, and Stamford D. Smith	277
Investigations Concerning the Taxonomic Status of the Sea Pen Ptilosarcus gurneyi (Cnidaria, Pennatulacea) Robert E. Batie	290
Reactions of Canada Geese to Reservoir Impoundment on the Snake River in Washington L. W. Gibson and I. O. Buss	301
Bacula of Two Western Moles Chris Maser and Cheri Brown	319
Tolerance of Lodgepole and Ponderosa Pine Seeds and Seedlings to High Water Tables P. H. Cochran	322
Radiative Temperatures in the Willamette Valley Lloyd W. Gay	332
The Glacial Geomorphology of the Puget Lowland, Washington and British Columbia: Further Comments and References David M. Mark and Peter M. Ojamaa	336

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